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A CRITIQUE ON THE PHASE THEORY OF LOCUSTS

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IN the course of studies on the ecology and epidemiology of the Australian Plague Locust, *Chortoicetes terminifera* (Walk.), extending over a period of some ten years, the author became increasingly convinced that the concepts and terminology of Uvarov's Phase Theory were often so ambiguous and vague as to be prejudicial to clear thinking. It also appeared that the content of the Phase Theory had been gradually extended to cover phenomena which could be more profitably studied and described within a different framework and by a different terminology.

These opinions were reinforced when the author undertook a study (unpublished) of adult phase differences in *Chortoicetes terminifera* and the related *Austroicetes cruciata* (Sauss.), and he was accordingly led to make a critical reexamination of the Phase Theory on the basis of all the available literature. It is the purpose of this paper to record the results of that review.

In order to present in a readily accessible form the major part of the relevant factual material, it has been thought advisable to give a somewhat lengthy account of the history of the development of the Phase Theory from its first publication up to 1947, at which time the manuscript of this paper was completed. This course seems all the more necessary since many of the aspects to which special reference will need to be made are given little prominence in existing accounts of the Phase Theory. The history is followed by a detailed discussion of the basic concepts and terminology, and by the conclusions to which the analysis as a whole has led. Of papers published since 1947, those available to the author do not call for any revision of these conclusions.

To avoid confusion between references to page numbers in other publications on the one hand, and cross references within the present paper on the other, round brackets have been consistently used for the former, and square brackets for the latter.

HISTORICAL DEVELOPMENT OF THE PHASE THEORY

The Period up to 1928

The Phase Theory was first propounded by Uvarov (1921), following the failure of his attempt to provide a basis for the rigid taxonomic separation of the supposed species *Locusta migratoria* L., *L. danica* L., and *L. migratorioides* R. & F. Although the theory was presented in outline only, and some of the ideas comprising it are now known to have been fallacious, nevertheless this first statement of the theory is important as indicating the class of phenomenon which its originator intended it to cover. The theory was intended to explain "the problem of the inter-relations of *migratoria*, *danica* and *migratorioides*" (p. 153), which could not be separated specifically, and represented "taxonomic units of lower grade than the

species" (p. 153), connected by transitional forms. The names of various infraspecific categories were reviewed, and finally the term "phase" was chosen as the most appropriate by which to designate the forms under consideration. The phases were designated by the old specific names prefixed by "ph.", or simply as the "gregarious phase" (or "swarming phase") and the "solitary phase."

In their typical development the phases were distinguished on the now well-known morphological and color characters of adults and nymphs, and on the degree of sexual dimorphism in size. With these physical differences are correlated biological differences, of which the chief are the gregarious and migratory behavior of *migratoria* and *migratorioides*, as against the non-gregarious, sedentary behavior of *danica*. A supposed difference in embryonic development has not been confirmed by subsequent observations. Phase *migratoria*, and probably phase *migratorioides*, has characteristic and restricted "permanent breeding grounds," whereas *danica* is much more generally distributed.

Field observations by Uvarov, and laboratory experiments of Plotnikov, convinced Uvarov that in succeeding generations ph. *migratoria* can be transformed into ph. *danica*, and vice versa; that is, the progeny of typical *migratoria* can be *danica*, and the progeny of typical *danica* can be *migratoria*. Phase *migratorioides* was regarded as a further modification of *migratoria* in the direction opposite to *danica*. The conditions responsible for the transformation were at this stage unknown, but it was suggested that transformation from the solitary to the gregarious phase was much favored, and probably caused, by oviposition of the solitary phase under conditions like those of the permanent breeding grounds of the gregarious phase. When this takes place, the multiplication and eventual emigration of the locusts are favored, for "the gregariousness of the *migratorioides* phase is, of course, one of the causes of a rapid increase in the number of individuals and swarms . . ." (p. 154). No grounds were given for the statement just quoted. After emigration, "the number of locusts in the breeding grounds drops suddenly to a minimum, and scattered swarms of the gregarious phase, as well as the progeny of individuals of the solitary phase, cause the gradual increase in the number of swarming individuals, and after a few years a new emigration occurs" (p. 155). From this it is concluded that "the periodicity of locust invasions is caused entirely by the wonderful phenomenon of the transformation of a swarming locust into a solitary, harmless grasshopper" (p. 155).

Observations of J. C. Faure, which Uvarov quoted, showed that two forms, quite analogous to the phases of *Locusta migratoria*, exist in *Locustana pardalina* (Walk.). These differ in their morphology, color, and behavior, and the observations indicated that the solitary phase (ph. *solitaria*) can transform, in succeeding generations, into the gregarious phase (ph. *pardalina*). According to Uvarov, this gave "very strong support to the theory of phases as a direct cause of the periodicity" (p. 159).

In this early stage of its development, the Phase Theory is reducible to three basic propositions:

1. In each of the locusts *Locusta migratoria* and *Locustana pardalina* there are two distinct forms of infraspecific status—the "phases"—which are connected by transitional forms, and are mutually transformable in successive generations.
2. The transformation from the "solitary phase" to the "gregarious phase" takes place most readily in the restricted "permanent breeding grounds" of the gregarious phase.
3. The transformation of the phases is responsible for the periodicity of locust invasions, because the gregarious phase is capable of more rapid multiplication than the solitary phase, and is migratory, whereas the solitary phase is sedentary.

It should be noted that the phases were defined on characters of structure and color, just like any other taxonomic unit, although it was pointed out that, as in the case of subspecies, there were intermediate forms that could not be assigned to either phase. The biological characters of gregariousness, etc., were clearly supposed to be closely linked with the physical characters, so that the former could be inferred from the latter, just as the biological characteristics of a sufficiently studied species can be listed when the species has been determined on diagnostic physical characters. On no other assumption would it be possible to ascribe the periodicity of locust invasions to the transformation of phases, when phases are defined on physical characters. However, it is implied that, to merit the appellation "phase," an infraspecific category must possess the distinctive relation to the opposed but mutually transformable states of

migratory gregariousness and sedentary isolation, respectively.

In his second paper dealing with phases, Uvarov (1923) suggested that the forms previously recognized as *Acridium flaviventre* Burm. and *Acridium coangustatum* Lucas represent the respective solitary phases of the species *Schistocerca gregaria* Forsk. and *Nomadacris septemfasciata* Serv., since they were always found singly, and bore much the same morphological relation to the forms of these species found in swarms as the solitary phase bore to the gregarious phase in *Locusta* and *Locustana*. These suggestions have been confirmed by Johnston (1926) and others, and observations on other species of locust by numerous authors have demonstrated in all of them the same polymorphism, bearing the same relation to gregariousness and migration.

Faure (1923) showed, by cage experiments on *Locustana pardalina*, that the cause of phase transformation, about which Uvarov had been uncertain, is the degree of crowding of the nymphs. That is, nymphs with the coloration of the gregarious phase (Faure used the term "swarm phase") develop the coloration of the solitary phase, after one or more moults, if they are separated from their fellows and maintained in isolation or near-isolation; and solitary phase nymphs develop the coloration of the gregarious phase if a large number are confined in one cage. This conclusion was fully substantiated by more detailed experiments (Faure, 1932), on the same species, and on *Locusta migratoria* and *Schistocerca gregaria*, and has been confirmed by many other authors for the same and other species. It permitted a clearer definition of the process of transformation in the field, which consisted (Faure, 1923) in a multiplication of the solitary phase in the "natural breeding grounds" of the locust, and the gathering of the insects into loose swarms, in which the transformation of color, and thus of phase, took place as in the cage experiments. Faure adopted essentially the same attitude as Uvarov with regard to the connection between phase transformation and the periodicity of outbreaks. He stated (1923, p. 21): "As Dr. Uvarov has well pointed out, the insect succeeds in maintaining itself during the years when no swarms occur, by living as a solitary grasshopper. As far as our brown locust is concerned, this explanation of its periodic abundance is no longer a theory but an established fact."

In the same paper of 1923, Faure called attention to the fact that the progeny of the gregarious phase can be distinguished from that of the solitary phase immediately on hatching by its black color, which had thus been "inherited" from its parents.

In his book *Locusts and Grasshoppers*, Uvarov (1928) summarized the findings of himself and others with regard to phases in locusts, and discussed various criticisms of the Phase Theory that had meanwhile been published. At the same time he offered certain new suggestions with regard to the mechanism of phase transformation and its relation to the periodicity of outbreaks. In this publication we find the first hint of an inconsistency with regard to the definition of phases which has since become much more serious and confusing. Thus on p. 147, and again on p. 159, the conception of phases was introduced in the same way as in previous papers, emphasis being placed primarily on structural and color differences, with which the biological differences were assumed to be correlated. But on p. 167 we find the statement ". . . it must never be forgotten that the main and principal difference between the phases lies in their bionomics, while their morphology is only the apparent result of some deep physiological differences."

Starting from the observations of Faure (1923) and Plotnikov (1927) that phase transformation depends upon population density, and with the general observation of much greater locomotor activity in the gregarious phase, Uvarov suggested that the prominence of black pigment in the hoppers of the gregarious phase should be ascribed to the accumulation of certain metabolites as a result of the high activity. Further, the black cuticular pigment would increase the body temperature of such hoppers and thus lead to still greater activity, so that a "vicious circle" would be formed, and "the species involved in it must progress in the direction of further development of the swarming phase" (p. 161). Also, because the gregarious phase appears as a consequence of crowding, and gregariousness implies the maintenance of crowding, "this process can only increase in intensity, and not decrease, no matter what the other conditions are . . . " (p. 161). Transformation into the gregarious phase leads to emigration. Since "as a rule only such years of migration and of the appearance of swarms in unusual regions are recorded as the years of appearance of locusts, and they

serve to calculate the periodicity" (p. 161), it therefore followed that phase transformation was responsible for the periodicity. However, there are several indications in the book that Uvarov also believed that transformation into the gregarious phase results in an increase in reproductive potential, and thus in an accelerated increase in the *general* population level, not merely a local increase in population resulting from migration. This would be in agreement with the views already quoted from his 1921 paper, and may be illustrated by the statement (1928, p. 248): "An increase in numbers is followed by the appearance of the swarming phase, and the curve [of numbers] starts to rise suddenly. Then an emigration follows. . . ". In a later contribution on the subject (Uvarov, 1937, p. 11), this point of view was abandoned.

Uvarov's book proved a tremendous stimulus to locust research all over the world, and an increasing number of papers on phases was published every year, reaching a maximum between 1934 and 1939. These studies resulted in much elaboration of detail, but contributed few really fundamental ideas to the Phase Theory, which may be said to have reached maturity with the publication of Uvarov's book. It will be convenient to study this later history under the following three heads, representing natural divisions of the accepted field of the theory:

1. the characterization and differentiation of the phases;
2. the mechanism of phase transformation in the field and the laboratory; and
3. the relation of the phases to the development of outbreaks and their periodicity.

Characterization and Differentiation of the Phases

In a general discussion of locust phases and their interrelations, Uvarov and Zolotarevsky (1929) moved still further from the original mainly morphological conception of phases. They stated (p. 261): "Biological differences are, of course, of primary importance, but the conception of phases in the minds of most workers remains mainly morphological, and they are trying to find absolute characters in the structure and color that would enable one to refer each specimen to a definite phase." They referred to the phase of a species as its "biological status," and elsewhere spoke of "biological phases" (p. 263). Also: "it would be futile to attempt to identify phases of locusts on the bases of the morphological and color characters of the specimens" (p. 264). However, these strictures are not directed so much against the use of physical criteria in separating the phases, as against their use in species or subspecies for which the physical characteristics of swarming and non-swarming material have not yet been properly established.

In accordance with their trend away from the taxonomic aspect of phases, Uvarov and Zolotarevsky proposed the use of the now widely accepted general terms, *solitaria*, *gregaria*, and *transiens*, to be applied to the phases of all locusts without regard for nomenclatural priority. Although these terms were not regarded as taxonomic in the ordinary sense, they were latinized and printed in italics. "*Phasis solitaria*" was to be applied to "the extreme form" represented by isolated individuals that could have had no immediate swarming antecedents, and "*phasis gregaria*" to "the extreme form found in dense, large, emigrating swarms." "*Phasis transiens*" would cover all the intermediate forms occurring "when the species is on the increase and its individuals are beginning to form loose aggregations, or on the decrease, and the swarms are becoming loose and tend to scatter . . ." (p. 262). It was subdivided into ph. *congregans* and ph. *dissocians*, terms that could be used in place of *transiens* when the direction of change of the phase of the material was known. Uvarov's original ph. *migratorioides* became the ph. *gregaria* of a distinct subspecies *migratorioides* R. & F. within *Locusta migratoria*, of which other subspecies were also recognized.

Zolotarevsky (1929), in a study of the phases of *Locusta migratoria migratorioides* and *L. migratoria capito* Sauss., determined the length of the tegmen, and the values for the ratios of length of tegmen to length of hind femur (E/F), width of pronotum at the point of greatest constriction to greatest breadth of head (M/C), and height of pronotum to greatest breadth of head (H/C), for a number of series of locusts classified as *gregaria* and *solitaria* respectively, and on the basis of these measurements he characterized the two phases by mean values for the ratios, and by ranges of the absolute values for tegmen length. It is not clear upon what basis the initial classification into *gregaria* and *solitaria* was made. Uvarov (1921) had classified his *migratoria* and *danica* material on physical characters, so that the mean values of his two ratios for "all *danica*" and "all *migratoria*"

could only be regarded as giving quantitative precision to this classification without changing the basis of it. Zolotarevsky, however, especially in view of the emphatic statements of Uvarov and Zolotarevsky (1929), probably classified his material in the first instance according to whether it came from swarms or from non-swarming populations without immediate swarming antecedents. In that case, his tables represent a genuine correlation between the degree of gregariousness and physical characters. The phase *gregaria* was found to have an E/F ratio always greater than 2.0. Phases *solitaria* and *transiens* were not separated morphometrically. Zolotarevsky also introduced a method for distinguishing the phases *congregans* and *dissocians* on their physical characters, which he elaborated in subsequent papers.

N. B. The symbols used in the present paper for various bodily dimensions are those recommended by the Third International Locust Conference in 1934, and do not necessarily correspond with those used by the authors whose work is discussed.

Faure (1932) showed very clearly that he regarded the phases as the morphological and color *forms* appropriate to locusts living in swarms and in isolation respectively. Thus he stated (p. 299): "the phase *solitaria* is the *form* [italics mine] living in isolation . . . and the *type* [italics mine] found in large swarms is called the phase *gregaria*." Again (p. 302), ". . . attempts were made to produce the phase *gregaria* out of *solitaria* in three different ways. . . . The results of these experiments may be judged by two different standards: the coloration of the hoppers, and the biometrical measurements of the adults." These are only isolated quotations, but the same point of view pervades the whole paper, as well as all subsequent publications of Faure (1933, 1935, 1943a, etc.). In view of this emphasis on structure and color in the definition of the phases, it is of interest to note that Uvarov (1937) was able to say of Faure's experiments that they had "established the existence of phases as a definite fact" (p. 1). As standards of comparison in determining the effect of his experiments on the adult phase characters, Faure used morphometric data from two main sources, namely, isolated individuals taken at widely separated localities over a long series of years, and specimens "of the extreme swarming phase" from a number of swarms from different outbreaks. Unfortunately, selection was made among the material from swarms on the basis of morphology. Thus material from "swarms of adults that were encountered during the last four or five years" was not used, because these swarms "all consisted of insects of the *transiens type* [italics mine]" (p. 312). Because of this double criterion used in classifying his basic material, the mean values obtained for the two groups cannot be regarded as giving a pure correlation between degree of gregariousness and physical characters, but represent, to some extent at any rate, merely a more precise, numerical statement of the original basis of classification.

It will be noted that Faure's basic standards do not show the range of variation that can be expected to exist between the means of different series of isolated specimens, and between the means of series from different strongly migrating swarms. All the data are lumped into the two categories, yielding means which are attributed to "extreme *solitaria*" and "extreme *gregaria*" respectively, whereas actually they can only represent "average *solitaria*" and "average *gregaria*." The failure to give any indication of range made it impossible for Faure, and later for du Plessis (1939), to state whether any given series of locusts, either collected in the field or bred in the laboratory, had actually reached a condition that could be called *solitaria* or *gregaria*, and Faure had to content himself with such expressions as "varying strongly towards *gregaria*," etc.

Faure's work demonstrated the great importance of absolute size, of which tegmen length was used as an index, as a phase character in *Locustana pardalina*, and the fact that the ratio E/F was less useful than any of the others in distinguishing the phases of this species. It showed also that indications given by the color of the hoppers and the morphometric characters of the adults were not very closely correlated. Thus the hoppers of one series of *Locustana* were recorded as 99 per cent *gregaria*, whereas the adults produced from them were only about half way from *solitaria* to *gregaria* on the criteria of tegmen length and E/F.

In a further study of phases in *Locusta migratoria capito*, Zolotarevsky (1933) introduced the new ratio: length of pronotum/greatest width of head (P/C). He adopted E/F as the main criterion in classifying his material with regard to phase, and regarded the other ratios as providing supplementary evidence. However, the variation of the pronotal ratios was not closely correlated with the variation of E/F. Zolotarevsky was able to show

that locusts submitted to low humidity during their development have a higher E/F ratio than those reared at continuously high humidity, although the difference is not nearly as great as that between the phases. The pronotal ratios are not affected unless the period of dryness is prolonged. Further, brown individuals reared under humid conditions have a higher E/F than green individuals, although there is no difference in the pronotal ratios. Brown individuals submitted to prolonged dryness show a greater lowering of the pronotal ratios than green individuals similarly treated. These observations are important as showing that the chief distinguishing characters of the phases are subject to modification by factors other than population density. Similar observations were subsequently made by a number of other authors. This immediately introduced complications in the characterization of the phases. Zolotarevsky proposed to regard as "typical" *solitaria* only such locusts as had certainly developed in isolation, and had not been subjected to prolonged dryness. Such individuals showed a mean value for E/F considerably lower than the value previously adopted for phase *solitaria* (Zolotarevsky, 1929). Nevertheless (p. 130), locusts in which E/F had been elevated by dry conditions into the range characteristic of ph. *congregans* should still be regarded as *solitaria* (presumably not "typical") if they had certainly developed in isolation, "d'autant plus que la conception de la phase *congregans* comporte la condition de l'accumulation des larves, aboutissant ou non au comportement grégaire."

At the Third International Locust Conference held in London in 1934, methods of calculating average morphometric ratios for series of specimens, in connection with phase studies, were discussed, and the following resolution was carried (see Conference Proceedings, Resolution 3(e)3): "The true average ratio is obtained by calculating the ratio of the totals of the actual measurements and not the average of the individual ratios." This statement has been quoted with approbation by several subsequent authors (e.g., Lean, 1936; Jannone, 1938), sometimes with reference to the Conference resolution as their authority, and sometimes without. Other authors (e.g., Rubtzov, 1935; du Plessis, 1939; Lea, 1938) have tacitly disregarded it, and used the average of the individual ratios. To my knowledge it has never been openly challenged. It was repeated unchanged as Resolution 4 (b) of the Fourth International Locust Conference, Cairo, 1936. The validity of the statement will be examined in a later section of this paper [p. 390].

Michelmore and Allan (1934), in a study of the phases of *Nomadacris septemfasciata*, classified their adult series into *gregaria* and *transiens* according to its degree and history of gregariousness, and based all their series means upon individual ratios. This permitted the calculation of the standard errors of the means, from which the significance of differences between series could be determined. In this respect the procedure of these authors was the most satisfactory since Gause's (1928) statistical analysis of the data on *Locusta migratoria* collected by Uvarov (1921), Plotnikov (1927), and Makalovskaja (1925). However, Michelmore and Allan did not attempt to characterize the two phases by either ranges or means for any of the measures they employed. They pointed out some remarkable color variations in the adults, which were to be ascribed partly to phase differences and partly to ageing, and recalled the earlier observations of Johnston (1926) on color changes in adult *Schistocerca gregaria*. In the latter species young adults produced from swarming hoppers are pink, while those produced from non-swarming hoppers are gray.

Johnston (1934), without quoting supporting data, gave the following E/F ratios for *Locusta migratoria migratorioides*: ph. *solitaria*, 1.70–1.80; ph. *transiens*, 1.80–1.90. Presumably ratios above 1.90 were regarded as *gregaria*. This was the first attempt to give limiting ranges for all three phases of any locust.

Pasquier (1934), in a paper on *Dociostaurus maroccanus* Thnb., introduced the new measure, width of mesosternum (S), and showed that the ratio E/S provides a wider contrast between material from swarms and non-swarming populations than any other ratio.

Rubtzov (1935), in a paper entitled "Phase Variation in Non-swarming Grasshoppers," was the first author to extend the concepts of the Phase Theory to insects other than the gregarious locusts. However, although he referred to the species studied as "non-swarming" and "non-gregarious," he stated that *Aeropus sibiricus* L. "has been occasionally observed to fly in swarms" (p. 500), and that all of six species in which phase variation is quite noticeable (including *Chorthippus albomarginatus* de Geer, on which most of his observations were made) "may occur in bands" (p. 500). It is

possible that he was not using the term "band" in the accepted sense, and meant only a dense patch of the insects in which true gregariousness was not exhibited.

Rubtzov noted that in *Chorthippus albomarginatus* considerably more black pigment is present in hoppers and adults from dense populations than in those from sparse populations, and that in rearing experiments the amount of black pigment could be varied by varying the density of the hoppers in the cages. He termed the darkest individuals "*gregaria*," the palest "*solitaria*," and intermediate types "*transiens*." This is an extreme example of the "physical" approach to phase differentiation, and a clear departure from previous practice, in which the phase *gregaria* was always taken to be the form occurring in dense, gregarious swarms, even if it was subsequently defined on morphological and color characters and recognized by these. There is no reference to gregariousness or swarming in any of the material analyzed by Rubtzov. Moreover he states (p. 512): ". . . in the field in the extremely dense populations . . . not more than 70–80% of the individuals can be classified as ph. *gregaria*." It is clear that Rubtzov's "phase *gregaria*" was applied to insects which might be regarded as ph. *transiens* under the accepted terminology, but certainly not as ph. *gregaria*.

In determining what morphometric characters were to be associated with his phases, Rubtzov made a phase classification of mixed adult material on the basis of coloration, and computed means for E, F, and E/F for the resulting groups. Phase "*gregaria*" was found to be larger than phase "*solitaria*," with a higher E/F ratio. Rubtzov admitted (p. 515) that this procedure is "not quite correct," inasmuch as it only establishes a correlation between the color classification and structure. Afterwards, more or less by way of confirmation, mean measurements and ratios were calculated for adult material from dense and sparse field populations, and it was shown that the former had the higher values. In the morphometric work the mean of the individual ratios was used, permitting the calculation of the standard error of the mean, and the determination of the significance of differences between groups.

Chopard (1935) demonstrated the existence of phase variation in an entirely different family of Orthoptera, namely in the Tettigoniidae. In *Barbitistes fischeri* Yersin and *Orphania denticauda* Charp. abnormally dense adult populations have occurred from time to time in France, and in these populations very dark forms are common. It has not been stated whether the insects show actual gregariousness, but they are more active than those of sparse populations. In the case of *Barbitistes*, the dark form had been described as *B. berenguieri* Valéry-Mayet. Chopard contented himself with concluding that these forms were an example of phase variation analogous to that in locusts, and did not attempt to apply the phase terminology.

Lean (1936) explored methods of separating the phases of *Locusta*, especially *congregans* and *dissocians*, on morphological and color characters, and gave rough ranges and means for *solitaria*, *gregaria*, and *congregans*. He attempted to use a "phase graph," in which tegmen length was plotted against femur length for equal ranges of E/F, as the basis of a separation between the phases *dissocians* and *congregans*. Although his conclusions could not be confirmed by later workers (cf. du Plessis, 1939; Kennedy, 1939), the curves themselves show a number of points of interest. Thus, within the males of any one series of locusts, taken at one time and place and of uniform origin, those individuals with the highest E/F ratio show a reduction in the absolute value of F, and may even show a reduction in E; whereas, if we compare males of different series, those series with the highest mean E/F have the *highest* mean values for E and usually for F.

In a study of *Locusta migratoria manilensis* Meyen, Uvarov (1936) presented morphometric data for a number of series from different localities, which he assigned to one or other of the phases. By averaging the data for these series under the headings of *gregaria*, *transiens*, and *solitaria*, he obtained mean values for each phase, which he then used in a comparison of *manilensis* with the other subspecies of *L. migratoria*. Unfortunately, in most of the series assigned to one or other phase, no indication is given as to whether the material was derived from swarms or from a non-swarming population, and several statements show clearly that the structure of the insects had been used as the main criterion in classifying them. Thus we have the statement (p. 102): "Some specimens of the ph. *transiens* from Annam have been received . . . but without any definite data as to their origin." In Malaya "a small incipient outbreak occurred . . . in 1930 . . . "; the adults "*proved to be* [italics mine] of the ph. *transiens*. . . ." (p. 101).

Even cage-bred material has been classed as "ph. *transiens*." All these series have been included in Uvarov's table (p. 93), so that the morphometric characters of the phases of this subspecies are derived largely from material classified on the very basis which the table itself is supposed to establish for the first time. This procedure is in conflict with the recommendations made jointly by Uvarov and Zolotarevsky (1929) with regard to the importance of establishing the biological status of material of each subspecies before any attempt is made at a morphometric characterization of its phases.

Similar objections apply to certain statements made by Uvarov and Hamilton (1936) with regard to morphometric characters in an Algerian race of *Locusta migratoria*. They stated, for example, (p. 87): "... in the F_7 most of the ratios approached very closely those typical of the ph. *gregaria*." Since the Algerian race is not known to swarm, and its subspecific position could not be established even after the work here described, it is difficult to see on what basis the above statement could be made. [This race was subsequently referred to *L. migratoria cinerascens* F., by Capra (1946).]

Husain and Mathur (1936b) showed that the typical color pattern of the phase *gregaria* can be produced in isolated hoppers of *Schistocerca gregaria* by an excess of CO_2 in the atmosphere of the breeding cage; but such individuals, upon becoming adult, show the morphometric ratios characteristic of the phase *solitaria*. In a second paper (1936a), the same authors characterized the types of hoppers produced under different experimental conditions of isolation or crowding as "green type," "intermediate type," or "black type," and thus avoided committing themselves to all the implications involved in the use of the phase terminology.

Butler and Innes (1936) showed that in *Locusta migratoria* the basal metabolism of phase *gregaria* is almost double that of phase *solitaria*. Strelnikov (1936), working on the same species, showed that ph. *gregaria* has a lower specific gravity than ph. *solitaria*, partly because of its lower water content, and partly because of the greater development of air sacs in the tracheal system.

Key (1936), in a theoretical discussion of activity in crowded and isolated locusts, suggested that the most significant difference between the phases was in nervous excitability, or irritability. This concept was confirmed and extended by Kennedy (1939) and Volkonsky (1942).

At the Fourth International Locust Conference, held in Cairo in 1936, two resolutions were passed which are of interest from the point of view of this discussion (see Conference Proceedings, 1937). Resolution 2 (1) reads as follows: "It has now been established by scientific research that a number of species both of locusts and of grasshoppers occur in two phases each of which is capable of transforming itself into the other. The first of these which is relatively harmless, is the solitary phase (*ph. solitaria*), the second, which is dangerous, is the gregarious phase (*ph. gregaria*)." This resolution implies endorsement of Rubtzov's use of the term "phase *gregaria*" with reference to the dark, long-winged forms found in dense populations of (non-swarming) grasshoppers—notwithstanding that the currently accepted definitions of "phase *gregaria*" (Uvarov and Zolotarevsky, 1929) and of "grasshopper" (Uvarov, 1928, p. vii) were not compatible with such use.

The second resolution of interest is Resolution 8, of which section (1) reads as follows: "It has long been known that scattered individuals of different locust species referable to the gregarious phase by reason of their structural characters, have been repeatedly found in the absence of swarms." The implication of this resolution is that, once the structural characters *typical* of individuals of a given species from dense migrating swarms are known, then the phase *gregaria* is defined in terms of those characters, and individuals possessing them are identified as ph. *gregaria* even in the complete absence of swarms. It is not clear whether the meaning of the resolution was intended to include the possibility that these scattered *gregaria* had never at any time been members of a swarm, but the remarks of Johnston (1937, pp. 2–3) certainly carry this suggestion. He reported the occurrence, in several different species and on several different occasions, of scattered individuals of ph. *gregaria* in places where no swarms had been recorded. This suggested that factors other than crowding may lead to the production of ph. *gregaria*. The tendency of later work has been to interpret such observations as indicating individual migrations by locusts that had developed in swarms elsewhere (cf. Waloff, 1940; Brédo, 1945). Even on this basis, it is clear that gregariousness can no longer be accepted as an invariable character of ph. *gregaria*, nor can long-distance migration be

regarded as inevitably dependent on gregariousness.

The first suggestions of long-distance migration by solitary locusts had come from Zolotarevsky, de Lépiney, and Dupont (1934), and Rao (1935). Further evidence, for both *Schistocerca gregaria* and *Locusta migratoria*, was provided by Rao (1937, 1938a). At first it was not clear from the accounts whether these "solitary" locusts possess the morphometric characters of phase *solitaria*, but this was placed beyond doubt by Rao and Bhatia (1939), Waloff (1940), Rao (1942), and Volkonsky (1942).

In a discussion of the cycle of events leading to outbreaks of *Locustana pardalina*, Faure (1937) stated (p. 804): "If the population is dense enough, compact swarms may be formed, and the transition into swarms may be said to be complete, although a critical study of the phase characters of the locusts would show that the swarms are composed of a mixture of *solitaria*, *gregaria* and *transitional* forms." Thus, not only can phase *gregaria* behave in a non-gregarious manner, but dense swarms can contain numerous individuals of phase *solitaria*. Subsequent observations by Kennedy (1939) showed that the mean morphometric ratios of a migrating swarm produced early in an outbreak cycle of *Schistocerca gregaria* were lower than the ratios of "extreme *solitaria*" studied by him, and similar (unpublished) observations have been made by the author on *Chortoicetes terminifera* (Walk.).

Rao (1937) suggested a characterization of all three phases of *Schistocerca gregaria* by ranges for E/F, *solitaria* having values of 2.05 and below, *transiens* 2.06–2.15, and *gregaria* 2.16 and above.

Zolotarevsky and Murat (1938) showed that in *Schistocerca gregaria* isolated specimens from the dry interior of Mauritania had a higher E/F ratio, and lower sexual dimorphism, than specimens from the moister coastal districts, i.e., they varied more towards the ratios typical of *transiens*. All these specimens were from sparse populations with no immediate swarming antecedents, and the observations confirmed those made earlier by Zolotarevsky (1933) on *Locusta migratoria capito*; they were repeated by Murat (1939). The females were more sensitive in their morphometric reactions to such climatic differences than the males.

Volkonsky (1938) crowded sexually immature adults of the phase *solitaria* of *Schistocerca gregaria*, and found that they developed the yellow coloration typical of phase *gregaria* as they matured. Of their progeny, 70 per cent were black, i.e., phase *gregaria*. Volkonsky regarded this as a change of phase in the adult stage, although the structural characters were of course unaltered, and characteristic of *solitaria*.

Lea (1938), working on *Nomadacris septemfasciata*, observed that individual (healthy) locusts are liable to drop out of swarms over areas of grassland. Such locusts, now isolated, very rapidly acquire the coloration and the shy, sedentary behavior typical of the phase *solitaria*, while retaining the high E/F ratio characteristic of *gregaria*. Instead of describing this as a change of phase, as Volkonsky (1938) had done in analogous circumstances, Lea introduced the term "solitary-living" to describe locusts of either phase that exhibit the coloration and habits typical of that mode of life. He also found that solitary-living locusts may be taken up by passing swarms, in which case coloration and behavior are rapidly transformed into those characteristic of swarming locusts. Moreover, adult solitary-living locusts ". . . may, at any time, congregate, and . . . this congregation is not confined to locusts of any particular morphological constitution" (p. 15). Thus the general behavior of adults is largely independent of their morphometric characters. In his morphometric comparisons Lea used the means of individual ratios.

Zolotarevsky (1938b) found that solitary-living adults of *Locusta migratoria migratorioides* of the ph. *gregaria* behaved in the same way as ph. *solitaria* in their response to microclimate, but also undertook more extensive movements in response to humidity differences at a distance of several kilometres. In an examination of morphometric and color differences between adults of the phases *congregans* and *dissocians*, he classified his material in the first place on the degree of gregariousness of the *hoppers from which the adults were produced*, and on whether the gregariousness was increasing or decreasing. Frequency distribution curves for E/F for such "*transiens*" series showed two peaks, one at the mean value for ph. *solitaria*, the other at the mean for ph. *gregaria*. The lowest numbers occurred in the intermediate E/F categories in the vicinity of 1.95–1.99. It is also suggested that after transformation from ph. *solitaria* has reached a certain point, it proceeds rapidly over to typical *gregaria*. It may be noticed that the phase categories are being used here in two conflicting

senses. First a *series* (population) was called "phase *transiens*" on the basis of hopper behavior, and then, when this series was analyzed morphometrically, it appeared that the majority of the insects were either phase *solitaria* or phase *gregaria*, relatively few being *transiens* in structure. When mean values for E/F were calculated for males and females separately in three series classed respectively as "*solitaria*," "*congregans*," and "*dissocians*," using only insects with E/F less than 2, the values for the males were found to be lower than those for the females in "*solitaria*" and "*congregans*," but higher in "*dissocians*." Since most reliable observations on *L. migratoria* have shown E/F to be lower for males than for females in *solitaria*, *gregaria*, and *congregans*, the reversal of this relationship in *dissocians* could be explained by assuming a more rapid transformation of females than of males in both directions, an assumption supported from other sources (cf. Zolotarevsky and Murat, 1938; du Plessis, 1939). A similar comparison of the sexes in the three groups, this time with reference to M/C, and to P/C calculated for different categories of E/F, led to similar conclusions, namely that "*dissocians*" can be separated from "*solitaria*" and "*congregans*" by making use of the different rates at which these ratios change in response to changes in the degree of gregariousness of the hoppers, and the different rates at which a given ratio changes in males and in females.

It should be noted that the statistical significance of most of the differences reported in this study is extremely doubtful. Moreover the suggestion that phase transformation of females is more rapid than that of males is in conflict with the fact that in the "*congregans*" series a much higher percentage of the males than of the females has a ratio greater than 2, i.e., has passed completely over into the phase *gregaria*.

Pasquier (1938) showed that there is a variation in size in *Dociostaurus maroccanus* and *Calliptamus italicus* L. in association with different habitats and seasons; he called this "ecological variation." In *C. italicus* the E/F ratio increases with increase in size, and to such an extent that false conclusions could be drawn regarding phase transformation. Pasquier suggested that the differences observed in the degree of expression of the characters of "extreme *gregaria*" of *D. maroccanus* from different outbreak areas may also be explained as ecological variation.

Jannone (1938), in a detailed study of the phases of *Dociostaurus maroccanus*, defined these purely on the basis of state of gregariousness, and proceeded to examine the physical characteristics of the resulting groups. The morphometric characters most useful as phase indicators were the absolute measurements, especially the total length of the body and the length of the tegmen, and the E/F ratio. All the absolute measurements were considerably greater in phase *gregaria* than in phase *solitaria*, especially in the male, and there was no overlapping between the ranges of individual values for the total length of the body or the length of the tegmen, in the two phases. Tentative ranges were given for series means of E/F in *solitaria* and *gregaria*, and here again there was no overlapping. The ratios P/C, H/C, and M/C were found to show little or no correlation with phase. Although Jannone measured as many as 1271 specimens, full use cannot be made of his work because of the impossibility of applying statistical criteria to his ratios, which were calculated from the totals of the absolute measurements. A study of color differences between the phases led to the conclusion that the color pattern, including the amount of black pigment, is not a pronounced phase character, even in the hoppers, but ph. *gregaria* adults show a diminished pattern contrast. Jannone confirmed and extended the observations of Paoli (1937) with regard to the higher fecundity of ph. *gregaria* in *D. maroccanus*. Females of this phase laid some 50 per cent more eggs per pod than phase *solitaria*; the number of ovarioles in the ovaries was the same in the two phases, but more eggs matured at one time in ph. *gregaria*.

Rao (1938b) extended observations made earlier by Roonwal (1936) on a new phase character in *Schistocerca gregaria*. He found that in ph. *gregaria* there were almost invariably 6 eye-stripes and 26 antennal segments, while in ph. *solitaria* there were 6 or 7 eye-stripes and 28 or 29 antennal segments.

Du Plessis (1939) carried out a most discriminating study of the adult phase differences in *Locustana pardalina*. His general viewpoint, although not stated explicitly, appears to have been that the phase of a given population is defined by its degree of gregariousness, and that the morphological characters of the adults are "an *expression* [italics mine] of phase" (p. 25). Thus the first object of the study was stated to be to ascertain "the amount of [morphological] variation in different phase groups of adults of known origin, and its

significance; and the best *indications* [italics added of phase, as revealed by this variation" (p. 25). The procedure adopted was to obtain mean values and variances for the different measurements and ratios for males and females of three "phase groups" designated respectively *gregaria*, *solitaria*, and *transiens congregans*. Material of doubtful status was then measured, and its means were compared with these standard means. The view then adopted seems to have been that the morphological indications are of greater importance than any field indications in establishing the phase, although this again was not explicitly stated (cf. pp. 48, 49, 51).

The "phase groups of known origin" are composed of the identical specimens used by Faure (1932). Regarded as standards of comparison, they are therefore subject to the limitations already indicated in discussing Faure's paper [p. 367]. In particular, they are so constituted that no estimate can be made of the variance between different series referable to one phase group. As a consequence, there is no basis for establishing a range of series means which could be regarded as permissible within any one phase group. When a series of unknown status is compared with the standards, a significant difference may be demonstrated between the means, but it remains impossible to determine whether this difference is of such magnitude as to exclude the unplaced series from the phase group with which it has been compared. This difficulty is well illustrated on p. 43 of du Plessis' paper. Du Plessis' position is further complicated by the fact that Faure used morphological criteria, to some extent at least, in selecting material for his standard groups, so that, for example, all material towards the lower limit of *gregaria* has been excluded from the "*gregaria*" group.

Both E and F were found to increase strongly from ph. *solitaria* to ph. *gregaria*. The ratio of sexual dimorphism in E ($E_{♀}/E_{♂}$) was found to decrease from 1.35 in *solitaria* to 1.03 in *gregaria*. This ratio was regarded as the best phase character, and "absolute size," of which E was taken as the measure, was placed second. In calculating mean values for E/F, the means of the individual ratios were used. This ratio increased from *transiens* to *gregaria*, but not significantly from *solitaria* to *transiens*. On the other hand, differences in hopper density, even within the category *solitaria*, could give rise to differences in absolute size and sexual dimorphism in the resulting adults.

In the course of laboratory breeding experiments, Vayssière and Lepesme (1939) showed that there is considerable variation in the nymphal coloration of *Schistocerca gregaria* under similar conditions of culture, and concluded that nymphal coloration is too "malléable" to be used in distinguishing the phases, at least in culture material. Moreover there was found to be a marked lack of correlation between the coloration of nymphs and the morphometric characters of the adults to which they give rise. The different morphometric ratios can also give contradictory indications, so that a value for E/F typical of ph. *solitaria* can be combined in the same insect with values for P/C, H/C, and M/C that are almost typical of ph. *gregaria*.

Murat (1939) found a wide range (1.80–2.17) in the values for E/F shown by sparse populations of *S. gregaria* with no swarming antecedents. The top of this range actually exceeds the lower limit proposed by Rao (1937) for the ph. *gregaria*. The higher values were explained on the grounds that the insects had developed under dry conditions, since the populations giving these values were actually less dense than those giving more typical *solitaria* ratios. Different generations had significantly different mean ratios (cf. du Plessis, 1939).

Kennedy (1939), working on the same species, found that sedentary, "near-*solitaria*" populations can show some yellowing on sexual maturation, and some pinkness when freshly moulted (p. 399). However, the yellow color of sexually mature ph. *gregaria* was found to be more amber-tinted. Kennedy's criteria of phase were not very explicitly stated, but it is clear that he regarded the degree of gregariousness as the fundamental one. His observation of a small swarm with mean E/F ratio lower than his "extreme *solitaria*" has already been mentioned. He concluded from this: "Thus it seems that the E/F ratio and other biometric features are unsafe criteria of phase unless account be taken of the stage of given individuals in the whole cycle of outbreak and non-outbreak years. . . A population which appears a fully gregarious swarm may be biometrically 'solitary' if it comes among the early swarms of an outbreak and *vice versa*" (p. 404). Kennedy's very detailed study of the behavior of all three phases led him to conclude that the behavior of even isolated *gregaria* differs from that of *solitaria*. The behavior of

gregaria is characterized by much increased excitability, and by the possession of a well-developed visual compensation reaction, which is sufficient both to keep members of a band together and to cause them to move parallel to one another; this is the "gregarious instinct proper."

Zolotarevsky (1939), in a study of the phases of *Nomadacris septemfasciata*, compared the morphometric characters of solitary-living locusts, believed to have developed from non-swarming hoppers, with material "provenant d'essaims en migration *et appartenant par conséquent à la phase grégaire*" [italics mine] (p. 72). Material of unknown origin was found to fall into one or other group (on the basis of E/F), and the whole material was then used to calculate mean ratios for ph. *solitaria* and ph. *gregaria*. E/F gave the best separation, followed by P/C, H/C, and M/C in that order. There was also the usual difference in sexual dimorphism, although it was not very marked.

Rao and Bhatia (1939) proposed three ranges of E/F as characterizing the phases of *Locusta migratoria* in India, namely: *solitaria*, 1.90 and below; *transiens*, 1.91–2.00; and *gregaria*, >2.00. These ranges differ from those advanced by Johnston (1934) for *L. migratoria migratorioides*.

Lea and Webb (1939) produced hoppers of *Nomadacris septemfasciata* with a color pattern almost indistinguisable from that of ph. *gregaria* by keeping green hoppers isolated in a hot exposed situation with a small amount of food. These hoppers were not noticeably more active than others which were isolated with plenty of green food and which remained green. The adults produced from them were, however, far from being morphometrically ph. *gregaria*. The authors have referred to the unsatisfactoriness of the categories *transiens congregans* and *transiens dissocians*, in view of the fact that a population may start by dissociating, and later begin to congregate (p. 26). Crowding of solitary-living adults in cages has produced the color of those found in swarms. Circumstantial evidence was obtained to indicate migration of ph. *solitaria* over a distance of a few miles. The attitude of these authors to the question of the definition of phase may be illustrated by the following quotation (p. 30): ". . . it has been shown that changes in phase are *accompanied by* [italics mine] corresponding changes in morphological characters. . . ."

Smit (1939), in a field study on *Locustana pardalina*, found that the length of the nymphal stage increases from about 25 days in ph. *solitaria* to about 40 days in ph. *gregaria*. Incomplete evidence suggested a larger number of eggs per pod in *gregaria*. This author, like Zolotarevsky (1938b) and others, applied the term "*transiens*" to mixed populations, in which, for example, individuals indistinguishable from ph. *gregaria* in hopper coloration might constitute a substantial proportion of the total.

Klingstedt (1939), in a general review of the Phase Theory from the point of view of its possible applicability to animals generally, stated (p. 4): "Das Wesentliche an den Phasen scheint überhaupt die eigenartige morphologische und physiologische Wirkung einer Stoffwechselveränderung zu sein, deren Ursache in erhöhter Aktivität liegt. . ."—brought about by mutual stimulation or, possibly, by other factors. In looking around for phase manifestations among insects other than locusts, this author used color and dimorphism in wing length as his chief criteria, and designated forms as ph. *solitaria* or ph. *gregaria* without any reference to their state of gregariousness or even activity. He assigned a phase interpretation to the phenomenon of brachypterism in such Acrididae as *Chorthippus albomarginatus*, *C. parallelus* Zett., *Podisma pedestris* L., and *Dendrotettix quercus* Riley, claiming that the longer wing is correlated with a shorter pronotum more suddenly widened behind. In *C. parallelus* the macropterous forms are said to be most numerous in dense populations; Rehn and Rehn (1938) are quoted as having made the same observation for *Dendrotettix quercus*, although I cannot confirm this from a study of their paper. It should be noted that in these cases we are unquestionably dealing with a very marked reduction in the length of the wings to the point where they become non-functional, whereas the general opinion with regard to the increase in E/F in locusts from ph. *solitaria* to ph. *gregaria* is that this change is due to a reduction in F rather than to an increase in E, relative to the general dimensions of the body (cf. du Plessis, 1939).

In a study of secondary differences between *solitaria* and *gregaria* males in *Dociostaurus maroccanus*, Jannone (1940) found surprising differences in characters usually regarded as not at all plastic, namely the subgenital plate and the epiphallus.

Waloff (1940), in a study of migration in *Locusta migratoria*, found that small groups and separate individuals of both phases migrated farther than large swarms—up to 1700 miles. When these groups

or individuals were of ph. *gregaria* they could represent detachments from large swarms, but they could also appear at times of local swarming in the outbreak areas when large swarms did not leave the immediate vicinity of these areas. Waloff concluded (p. 240) that ". . . long range migrations of phase *solitaria* occur in several, and perhaps in all, species of swarming Acrididae. . . . The ability to migrate is not restricted to phase *gregaria*. . . ." She used the value E/F = 2.00 as the boundary between *solitaria* and *transiens*, and 2.10 as the boundary between *transiens* and *gregaria*. Her attitude to the definition of phase is shown by her use of the phrase, "the degree of morphological modification *accompanying* [italics mine] phase transformation" (p. 238).

Volkonsky and Volkonsky (1940b), on the other hand, have stated that in *Schistocerca gregaria* migration of ph. *solitaria* is extensive, but not as extensive as that of swarms. Elsewhere the same authors (1940a) presented data showing that, in both sexes of this species, individuals with 6 eye-stripes have a higher mean E/F, and a lower E, than individuals with 7 eye-stripes from the same series.

In a study of eye size in relation to phase in *Locusta migratoria migratorioides*, Thomas (1941) established that the eye is relatively smaller in ph. *gregaria* in both sexes, and expressed this new phase character by the ratios E/D and C/D, D being the height of the eye.

Chauvin (1941) based his determinations of phase, in laboratory material of *Schistocerca gregaria*, upon nymphal and adult coloration. He stated that the eggs laid by females of phase *solitaria* require a temperature of 40°C. for hatching, whereas eggs from *gregaria* females hatch at temperatures below 30°C. Contrary to the results obtained by Smit (1939) on *Locustana pardalina*, the phase *gregaria* was found to develop more rapidly than *solitaria*; individuals of the former phase also weighed less and lived longer, ate much more food, had a lower mortality rate, and a thicker cuticle. *Gregaria* developed melanin in the integument, retained strongly the carotenoids, and especially the xanthophylls, of plants, and contained acridioxanthine in the hypodermis; *solitaria* on the contrary, had no melanin and little or no acridioxanthine, retained carotenoids poorly, and xanthophylls not at all. Even among the progeny of *solitaria* adults, kept completely isolated in green cages, 52 per cent showed a "*transiens*" coloration. A "*gregaria*" coloration could be produced by placing a single *solitaria* hopper in a crowd of the non-swarming *Cyrtacanthacris ruficornis*. Hoppers of typical *solitaria* appearance can occasionally give rise to pink adults with *transiens* morphometric ratios, and sometimes to adults with *gregaria* ratios. Females reared in crowds lose their acridioxanthine and their gregarious instinct as they become senile and may then be regarded as ph. *solitaria* (presumably notwithstanding the possession of *gregaria* morphometric ratios).

In this paper Chauvin uses the term "grégarisme" in a novel sense. Its normal meaning is rendered in English by "gregariousness." However, Chauvin uses it to cover the general characters of the phase *gregaria*: it is, in his own words (p. 235), "un phénomène *sui generis* qui survient chez les criquets groupés, et se manifeste par des modifications pigmentaires et physiologiques variées . . . un phénomène physiologique." For the term "gregariousness" in its usual sense, Chauvin uses "instinct grégaire" ("un phénomène de comportement psychologique"). He distinguishes four kinds of this "grégarisme," namely, "larvaire," "imaginal," "sexuel," and "résiduel." "Grégarisme larvaire" is the capacity of nymphs reared in a crowd to develop the black and reddish pigmentation characteristic of the ph. *gregaria*. "Grégarisme imaginal" is the capacity of the male to develop the yellow pigmentation when reared in a crowd. "Grégarisme sexuel" is the faculty possessed by the female of producing offspring of ph. *gregaria* if it is itself submitted to gregarious stimulation. "Grégarisme résiduel" is the tendency of isolated nymphs to remain or become ph. *gregaria* during their development, as a consequence of the "grégarisme" of their parents, and is calculated as 100 per cent minus the percentage of typical *solitaria* hoppers in the fifth instar. Much of this terminology is open to criticism, and in general it has not been followed by later workers.

In a later paper the same author (Chauvin, 1944) employed a biochemical estimation of acridioxanthine per 0.5 g. of body weight as a measure of his "grégarisme." Using an "index solitaire," which bore an inverse relation to the acridioxanthine content, he was able to show that this index was highest in locusts reared in isolation, and lowest in those reared in crowds. However, there was considerable variation in the "index solitaire" among locusts of similar external pigmentation and among locusts of different age, and no attempt

was made to establish critical values for the different phases.

Rao (1942), discussing the morphometric differentiation of the phases in *Schistocerca gregaria*, agreed with the conclusions of earlier authors (Zolotarevsky, 1938b; Vayssière and Lepesme, 1939) that "variations in the different characters do not appear to be linked together, but occur independently" (p. 248). Rao introduced the concept of the "biometrical facies" or "constitution" of a given locust population in contrast to the phase of an individual locust. Claiming (p. 249) that ". . . average biometric ratios . . . do not convey any idea of the extent of variation in regard to phase development in the population," he used a "biometrical index" (really a formula) to describe the biometrical facies. This formula shows the percentages of individuals classifiable, on the basis of their individual E/F ratios, as *solitaria*, *transiens*, and *gregaria* (using the E/F ranges assigned to each phase by Rao (1937)), along with the percentages with 6 and 7 eye-stripes. It has the form aS:bT:cG::p(6):q(7). It will be noted that this procedure represented an attempt to obviate the inconsistency, which has been referred to more than once already, whereby one and the same set of terms has been used for the "phase" of a population and for the different "phases" of the individuals composing it (cf. Zolotarevsky, 1938b; Smit, 1939).

Rao noticed a "remarkable parallelism" between the phases *solitaria* and *gregaria* in their life-cycles and migrations, the only difference being the greater activity of *gregaria*, which "owing to its occurrence in swarms is capable, under the influence of mob psychology, of reaching longer distances and covering wider areas" (p. 263). He showed that the value of the width of the head (C) as a phase character attaches only to the width at the gena. The width at the level of the eye (O) does not vary as between phases, and the ratio C/O increases from *solitaria* to *gregaria*.

Volkonsky and Volkonsky (1942) found that young adults of *Schistocerca gregaria*, derived from a swarm and with ph. *gregaria* ratios, but subsequently isolated from the swarm, show very little yellowing on reaching sexual maturity. In a second paper published in the same year, Volkonsky (1942) agreed with Waloff (1940) that migration is not a phase character, but held that it is more extensive in *gregaria* than in *solitaria* (cf. Rao, 1942; Volkonsky and Volkonsky, 1940b).

Faure (1943a) carried out a laboratory study of phases in an army worm, *Laphygma exigua* Hübn. Apparently unaware of the paper by Klingstedt (1939), Faure stated (p. 69): "There appear to be no references in the literature to the discovery of phases in any other group of insects" [than Orthoptera]. This quotation is of interest in demonstrating once again the crucial place accorded by Faure to color and morphology in his conception of phase. There are many species, widely distributed in the animal kingdom, which may be gregarious or non-gregarious according to their abundance or in relation to the reproductive cycle or seasonal conditions, and these differ in their behavior, physiology, and distribution according as they are gregarious or non-gregarious; but these species do not show morphological or color differences correlated with their degree of gregariousness.

Faure classified his larvae according to an arbitrary color scale connecting the extreme types found in isolated and crowded cultures, respectively. At the dark end of the scale, three color types, which were most common in crowded cultures, were classed as "phase *gregaria*"; and at the pale end, two, most common among isolated larvae, as "phase *solitaria*"; intermediate forms were classed as "phase *transiens*." There was no reference to the color of specimens found in swarms and in isolation in the field, and Faure's procedure here is subject to the same criticisms that have already been advanced in connection with Rubtzov's work (1935) on grasshoppers. When larvae reared in isolation were classified in this way, as many as 12 per cent had to be described as "*transiens*," although some of these, amounting to 2 per cent of the isolated larvae, were apparently indistinguishable from "*gregaria*." Of larvae reared in crowds, only 64 per cent could be classed as "*gregaria*," while 8 per cent were "*solitaria*." The larvae in crowds were more active than those in isolation, and the adult moths bred from crowded larvae were slightly darker than those from isolated larvae.

In a second paper, on a more strongly gregarious army worm, *Laphygma exempta* Walk., Faure (1943b) used the same method for establishing his categories of "*solitaria*," "*transiens*," and "*gregaria*," and in this case he got a rather better correlation with the state of crowding. All the crowded larvae were found to be "*gregaria*," and of isolated larvae 62.4 per cent were found to be "*solitaria*," 36.5 per cent "*transiens*," and 1 per

cent "*gregaria*." However, when isolated larvae were reared in darkness, 32 per cent were indistinguishable from "*gregaria*," and only 12 per cent were classed as "*solitaria*." Crowds were again noted to be much more active than isolated larvae. In *Spodoptera abyssinia* Guen., a noctuid of minor economic importance, marked color differences were also found between crowded and isolated larvae. Although, on the basis of these, categories designated "*solitaria*," "*transiens*," and "*gregaria*" were established, Faure stated (p. 15): "It is rather problematical whether one would be justified in describing this variation . . . as phase variation comparable with that of locusts and army worms . . . for this reason: the fundamentally important factor of increased activity appears to be lacking or very poorly developed in the crowds of this species." However important activity may normally be in the *mechanism* by which the morphological and color characters of the phases are produced, this was the first occasion upon which it had been suggested that this factor should be regarded as fundamental in the *definition* of the phases. Indeed, it had been claimed by several authors who had produced apparently typical phase *gregaria* in locusts reared under artificial conditions that little or no increase in activity was to be noted (cf. Lea and Webb, 1939; Chauvin, 1941).

Duck (1944) crowded nymphs of the non-swarming *Schistocerca obscura* (Fabr.) and found that they developed a color pattern similar to that of the phase *gregaria* in locusts—provided the temperature was not too high.

Husain, Lahore, and Mathur (1944), working on *Schistocerca gregaria*, found that locusts reared in isolation at 27°C. showed E/F ratios characteristic of ph. *solitaria*, but that those reared at 40°C. had ratios characteristic of *transiens* (using the criteria of Rao (1937)). On the basis of their isolation and nymphal coloration, all of these locusts would be referred to ph. *solitaria*, and the authors therefore asked (p. 111): "With what certainty can certain fixed values be assigned to the various biometrical ratios as criteria of the phases of the adults?"

In a field study of *Dociostaurus maroccanus*, Bodenheimer (1944) confirmed the observations of earlier authors regarding the larger number of eggs per pod laid by the phase *gregaria* in this species, and concluded further that in *gregaria* each female lays several egg-pods, each separated by a "maturation flight," while in *solitaria* one egg-pod is the normal number. He stated that this higher fertility of *gregaria* is associated with a higher general vitality, including a lower mortality rate, but he gave no evidence in support of this. In the following quotation (p. 84), Bodenheimer expressed particularly forcefully a conclusion to which his own work, as well as that of many of the authors already considered, must inevitably lead: "But it must always be retained in mind, that neither the morphological nor the chromatic characters of an individual or even of a population permit a conclusion on its behaviour. . . . The decisive criterium will always be the behaviour in the field and this may change within the same generation without leaving definite characters of form or color in the resulting adults."

In discussing the question of isolated locusts with phase *gregaria* ratios, Brédo (1945a) showed that individual *Nomadacris* that become detached from a flying swarm may travel up to 45 miles from the route taken by the swarm before alighting. Such locusts lose their swarming coloration within 3 to 4 weeks and, according to Brédo, should then be regarded as ph. *transiens*, notwithstanding their *gregaria* morphometric characteristics.

Matthée (1945), in an investigation of biochemical differences between the phases in *Locusta migratoria*, *Locustana pardalina*, *Laphygma exempta*, and *Spodoptera abyssinia*, as defined by Faure, found that in all species the uric acid content of the blood was higher in ph. *solitaria* than in ph. *gregaria*, while the fat content was higher in *gregaria* than in *solitaria*. Phase differences in lactic acid content, water content, and the pH of the blood were also established for certain of the species.

The same author (Matthée, 1946) confirmed the findings of Faure (1943b) with regard to phase variation in *Laphygma exempta*, including the occurrence of individuals of both "ph. *gregaria*" and "ph. *solitaria*" among material reared in isolation. However, by rearing larvae in isolation for three successive generations, Matthée was able to increase the proportion of "*solitaria*" to a maximum of 82 per cent. He found, further, that "*solitaria*" usually passed through five instars, and "*gregaria*" through six, while the width of the head capsule was significantly greater in "*solitaria*" than in "*gregaria*." In a further paper (Matthée, 1947), Faure's findings on *Spodoptera abyssinia* were confirmed; intensification of the *solitaria*

characters again proved possible by rearing successive generations in isolation.

In the most recent theoretical discussion of the Phase Theory, Zolotarevsky (1946) has exemplified once more that confusion of concepts and definition which has been referred to more than once in the preceding pages, and which is discernible throughout the history of the theory that has been presented. On p. 102 he has stated that density of population is "le facteur essential" in phase transformation, and that one cannot be sure that the morphological changes produced by manipulating such factors as humidity, temperature, food, stimuli, activity, or metabolism, are not "analogue mais . . . indépendante." Yet in discussing the evidence for migration of ph. *solitaria* over great distances (which he largely discounted) he did not hesitate to place absolute reliance upon the morphometric characters of the insects as evidence of their phase. Later he stated that the "nature" of the phenomenon of phases had not yet been defined, nor its place in the "cycle biologique" of living things. The studies carried out up to the present had provided plausible explanations of phase *manifestations*, but had not thrown light on "la notion du phénomène." The manifestations, singly or in combination, were widespread in the animal kingdom, but these were external expressions of deeper phenomena; the phenomenon of phases should be defined in terms of these deeper phenomena rather than in terms of the phase manifestations. Certain of the manifestations were not specific to phases, and the absence of some of the usual ones, including morphological differentiation, did not signify an absence of phase phenomena. (Here we have the complete antithesis of the viewpoint of Faure, for whom phase differences are preeminently characterized by a distinctive type of structural or color modification associated with population density.) Zolotarevsky concluded the theoretical part of his paper with the statement that "le phénomène des phases peut être désigné comme un état biologique instable des individus d'une espèce dont les variations se manifestent par leur physiologie, comportement ou aspect en fonction des modalités de leur interaction."

Michelmore (1947) stated (p. 332) that in *Nomadacris septemfasciata* hoppers of ph. *solitaria* "are sometimes slightly gregarious," and that a concentration of *solitaria* adults may behave as "a true swarm for a few days." He used the expressions "grasshopper phase" and "locust phase" as synonyms for ph. *solitaria* and ph. *gregaria*.

From a comparative histological study of the striped eyes characteristic of ph. *solitaria* in *Schistocerca gregaria*, and the unstriped eyes characteristic of ph. *gregaria*, Roonwal (1947) reached the following conclusions. In the unstriped eye a true apposition image is formed, which is sharply defined; the eye is adapted to vision under intense illumination. In the striped eye a pseudosuperposition image is formed, brighter and more diffuse than in the unstriped eye, so that movements, rather than discrete, sharply-defined images, are perceived; the eye is adapted to vision in subdued light. These characteristics of the eyes affect the clearness with which a hopper can perceive his fellows, thus influencing gregariousness; they are also correlated with the readiness with which *gregaria* hoppers move into open well-lit spaces, compared with the vegetation-frequenting ph. *solitaria*.

Murat (1947) reported "ph. *transiens*" adults of *Schistocerca gregaria* in which E/F had the value characteristic of ph. *transiens*, while the other morphometric ratios, the sexual dimorphism ratio, and the coloration were found to be very close to ph. *solitaria*.

The Mechanism of Phase Transformation

It will be recalled that at the time of the publication of Uvarov's book in 1928 the mechanism of phase transformation was visualized somewhat as follows: multiplication of ph. *solitaria* in special localities leads to crowding, which in turn leads to increased activity. High activity leads to the deposition of black pigment in the cuticle of the hoppers, as a result of which their body temperature (in the sun) is raised, and their activity is consequently still further increased. As a result of the crowding the gregarious instinct is awakened, and this perpetuates and increases the condition of crowding. Thus a vicious circle is set up which leads to the development of the characters of the extreme phase *gregaria*.

Faure (1932) ascribed the increased activity of crowds to mutual stimulation, chiefly tactile, and explained the metabolic effects of high activity by postulating a metabolite "locustine," which is produced in active hoppers or adults, giving rise, in the former, to the characteristic *gregaria* color pattern, and capable of being transmitted to the progeny of active adults in the egg-yolk. He as-

cribed the morphometric characters of ph. *gregaria* to mechanical effects of continual muscular contraction.

The assumption of an increased body temperature in black hoppers exposed to solar radiation was confirmed by Hill and Taylor (1933) and by Strelnikov (1936), but its significance in increasing activity was questioned by Key (1936), on the ground that what is gained toward the lower temperature threshold of activity might be lost at the upper threshold, when black hoppers could be expected to seek out shaded situations at a lower air temperature than pale hoppers. This point of view was to some extent confirmed by Kennedy (1939), although his data are not well adapted for a separation of activity effects due directly to body temperature from those due to increased excitability.

On the basis of field studies by Uvarov (1932) on *Dociostaurus maroccanus*, Zolotarevsky (1933) on *Locusta migratoria capito*, and others, Zolotarevsky (1934) was able to establish the general conditions of phase transformation in the special localities (outbreak centers) in which alone that transformation is possible. The first of these conditions is an unstable climate, allowing of tremendous increases in the locust population from time to time. As a rule, such increases do not in themselves produce the degree of crowding necessary for transformation into the ph. *gregaria*, and a further condition, namely, a restriction of favorable locust habitats to patches of limited area within a relatively unfavorable terrain, is required. These general conditions for phase transformation could take on very different forms according to the species of locust and the geographical region. Moreover, various other factors, such as the degree of synchronization of hatching, have a bearing upon the outcome in particular cases.

Very similar views on the general mechanism of phase transformation in the field were expressed by Uvarov (1937), although he tended to place greater emphasis upon a *reduction* in the size of favorable habitats resulting from adverse climatic factors, and the consequent active concentration of locusts into them. According to this scheme a period of favorable weather leads to multiplication; this is followed by an unfavorable period leading to restriction of the favorable habitats, concentration of the now large locust population within them, and consequent transformation into the phase *gregaria*. In this paper Uvarov repeated his earlier view that once phase transformation has commenced it is obliged to continue with increasing intensity, unless the swarms are broken up by external agencies; in that case the scattered remnants, no longer stimulated to activity by their fellows, revert to the ph. *solitaria*.

Detailed studies of the ecology of various species of locust in their outbreak areas by Smit (1939), Kennedy (1939), Volkonsky (1942), Bodenheimer (1944), and others, have largely confirmed the general theories of Uvarov and Zolotarevsky as summarized above, and have extended them in various directions.

Kennedy (1939), working on *Schistocerca gregaria*, was mainly concerned with the process of "concentration," as understood by Uvarov, and with its behavior consequences. He found that morphometric changes lagged behind activity changes, and activity changes behind changes in color and gregariousness, in both directions of phase transformation. He divided what he termed the "outbreak process" into three stages (p. 406): (a) "concentration," of which two distinct types were of significance; (b) "aggregation," defined as "the grouping of concentrated individuals in contact with each other so that fellow-individuals assume an increasingly important part in the sensory experience of each locust"; and (c) "gregarisation," defined as "the change of phase (appearance of gregarious behaviour and coloration), the result of intensive aggregation." Both concentration and aggregation were found to be produced entirely by external factors acting on each locust individually. The first stage in gregarization is habituation to fellow-locusts, and is passed through by hoppers that are exposed repeatedly to aggregation. It involves a discriminative refinement of the visual compensation reaction, which may be seen in crude form in ph. *solitaria* in its visual attraction to vegetation. In the second stage, activity and excitability gradually increase. If good habituation has been attained (first stage) before activity reaches a high level, bands leaving the zone of concentration would maintain their coherence. Activity could then increase still further, thus increasing migration range.

Volkonsky (1942) arrived at a conception of phase transformation in *Schistocerca gregaria* which differed in some important details from Kennedy's, but preserved the essential feature of a number of distinct stages, of which the major ones were readily reconcilable with those of Kennedy. In

particular, Volkonsky found both an interaction between hoppers, and a resulting increase in activity, at a much earlier stage in the whole sequence of events than did Kennedy. Zolotarevsky (1946) criticized both Kennedy's and Volkonsky's delimitation of stages, and proposed a formulation of his own involving three stages: "pullulation," "prégrégarisation," and "grégarisation."

Bodenheimer (1944), working on phase transformation in *Dociostaurus maroccanus*, was able to apply Kennedy's scheme with little modification. He found that in this species also "the morphological features of phase transformation lag very distinctly behind the transformation of behavior" (p. 77). The morphological changes also lag behind the increase in fecundity, to which, along with the increase in "general vitality" said to be associated with it [p. 377], Bodenheimer assigned an important role in the outbreak process in *Dociostaurus*. In this connection Bodenheimer has provided evidence in favor of an assumption made by Uvarov in 1921, but subsequently abandoned by him [pp. 364, 365, 366]. Bodenheimer stressed particularly the role of climatic factors in promoting or hindering such processes as aggregation, and thus influencing phase transformation in an indirect way.

Apart from these investigations of the normal course of events in the field, a considerable amount of laboratory and other work has been carried out with the object of elucidating the mechanism of phase transformation by analyzing the factors of crowding and high activity, and by inducing one or other aspect of phase transformation by artificial means. The first experiments of this kind were carried out by Faure (1932), who claimed to have shown that the color pattern characteristic of phase *gregaria* can be produced in isolated hoppers of *Locustana pardalina* that are forced into abnormal activity in a special apparatus. His findings were supported by Husain and Mathur (1936a), who showed, moreover, that the *gregaria* pattern can be produced by placing individual hoppers of *Schistocerca gregaria* in crowds of non-swarming grasshoppers. We have already noted that the same authors (Husain and Mathur, 1936b) found that the pattern of phase *gregaria* can be produced in isolated hoppers reared in an atmosphere containing about 3 per cent CO_2.

Johnston (1937) reported (p. 3) that "field observations in Uganda have suggested that food scarcity leading to movement may be sufficient to influence the phase of single nymphs [of *Schistocerca gregaria*] leading them to become in structure ph. *gregaria*." A tendency in this direction, produced by dry conditions, had already been found by Zolotarevsky (1933) in *Locusta migratoria capito* [p. 368], and was later confirmed by Zolotarevsky and Murat (1938) and Murat (1939) for *Schistocerca gregaria* [pp. 371 and 373]. Similarly, Lea and Webb (1939) produced "*gregaria*" hoppers by isolating green hoppers of *Nomadacris septemfasciata* in a hot exposed situation with a small amount of food [p. 374], and Husain, Lahore, and Mathur (1944) produced adults of *Schistocerca gregaria* with E/F ratios characteristic of the phase *transiens* by rearing hoppers in isolation at 40°C. [p. 377]. The suggestion of Pasquier (1938), that the different degrees of expression of the characters of "extreme *gregaria*" in material of *Dociostaurus maroccanus* from different outbreak areas may be due to "ecological variation," i.e., to the effects of physical factors and food supply, has already been mentioned [p. 372].

Chauvin (1941) criticized the work of Faure (1932) and Husain and Mathur (1936a), in which the *gregaria* coloration had been produced in isolated hoppers placed in an activating apparatus, on the grounds that in both cases these isolated hoppers were able to see other hoppers. His own work on *Schistocerca gregaria* had shown that the *gregaria* pigmentation can arise from the association of only two or three hoppers provided they can see each other. He carried out experiments of his own with an activating apparatus in which the individual hoppers were prevented from seeing each other, and found that ph. *gregaria* hoppers became *dissocians* as the experiment proceeded. On the basis of this result and of his observation that locusts in crowds were very little more active than isolated ones, he concluded that activity is only a result, and not a cause of "grégarisme." In support of this view, Chauvin pointed out that *Schistocerca gregaria* is the least active of the major locusts, and yet it develops the *gregaria* pigmentation more readily than any of the others. Further, the assumption that the close proximity of gregarious locusts will lead to increased activity was not supported by findings on other animals, in which activity is sometimes greater, sometimes less, in crowds. The high activity of locusts in the phase *gregaria* is, in fact, a character specific to this group. From these and other considerations, Chauvin concluded that the pigmentary phase differences in *Schistocerca gregaria* are not the con-

sequence of differences in activity, but are of the nature of a reflex response to sensory impressions of fellow locusts effected through nervous mechanisms, endocrine mechanisms, or both.

"Grégarisme larvaire" [p. 375] could be evoked by either visual or tactile impressions. In the case of visual impressions, *movement* of fellow locusts was necessary, and a factor of *recognition* was also involved, since only members of the Acrididae served to elicit the reaction. "Grégarisme imaginal" could be produced in adult male locusts of any phase subjected to crowding, even in the absence of females. It did not occur in castrated males, was the result of tactile stimulation received largely through the antennae, and probably depended upon an endocrine rather than a nervous mechanism. "Grégarisme sexuel" was due to stimulation of the female prior to oviposition, even in the nymphal stage. The longer the total period of stimulation, even at rather widely separated intervals, the greater the percentage of *gregaria* first-instar nymphs in the progeny. Chauvin favored some such explanation as the "locustine" theory of Faure (1932) for "grégarisme sexuel" and "résiduel."

It will not be possible to evaluate the significance of Chauvin's work in the present paper. Certain of his conclusions are arguable on various grounds, and further work on other species of locusts is clearly needed. There is no doubt, however, that he has indicated a possibility that could require a drastic revision of our views on the mechanism of phase transformation.

Following upon the suggestion by Faure (1932) that the structural characters of ph. *gregaria* may be due to the constant pull of the muscles upon the exoskeleton in an insect exhibiting a high degree of activity, Uvarov and Thomas (1942) studied the thoracic muscles of *Locusta migratoria*, and found that the muscles whose contraction might be expected to produce the deformations of the pronotum characteristic of the phase *gregaria* are those concerned in movements of the head and pronotum in relation to the body, and of the first pair of legs. The authors pointed out that in ph. *gregaria* much more time is spent in a horizontal position on the ground than in ph. *solitaria*, and that consequently more muscular exertion is required to support the large head; contraction of the muscles of the legs, including the first pair, must obviously be greater in ph. *gregaria* than in ph. *solitaria*.

The Relation of the Phases to the Development of Outbreaks and their Periodicity

In presenting his Phase Theory, Uvarov (1921, 1928) made it abundantly clear that he regarded the phenomenon of phase transformation as the fundamental cause of the development of locust outbreaks and their periodicity. Typical quotations illustrating this point of view have already been given [pp. 364, 365]. Briefly, phase transformation played this role because: (a) it resulted in an increased reproductive potential; (b) it resulted in migration and invasion of new areas; and (c) its nature was such that once it had commenced it was bound to continue with increasing intensity. The claim that transformation into the phase *gregaria* involves an increase in reproductive rate was later abandoned (Uvarov, 1937), although it has been substantiated since for two species of locust (see Bodenheimer, 1944; Smit, 1939). Ample evidence has already been quoted to show that migration is not an attribute peculiar to the phase *gregaria*, although it is more pronounced in that phase; migration, therefore, is not dependent upon phase transformation. Finally, as will be shown below, there is much evidence that phase transformation is readily arrested or reversed by various environmental factors.

Notwithstanding this weakening of the basis of the theory of the relation of phases to outbreaks, Uvarov's original views on this question have been restated with little modification, both by himself and other leading locust workers, right up to the present time. Thus Uvarov (1937) held that Zolotarevsky's field researches had "confirmed the connection between phase transformation and mass outbreaks" (p. 1), and that "the irregular periodicity of swarming in locusts cannot be studied without paying due regard to phases" (p. 6). Later (Uvarov, 1944) he wrote (pp. 97–98): "The periodicity of locust outbreaks is closely connected with the periodical transformation of the harmless solitary phase into the dangerous gregarious one. . . . The [phase] theory has supplied the key to the whole problem." Faure (1937) went even further when he stated (p. 799): "The phase theory is the foundation on which our present conceptions of locust biology rest."

This view of the crucial part played by phase transformation led to a redefinition, in terms of phases, of what had previously been referred to as the "permanent breeding grounds" of a locust. Thus the "outbreak areas," i.e., "des lieux où les

espèces d'acridiens vivent en permanence et d'où elles entreprennent leurs migrations pendant les années de développement en masse" (Zolotarevsky, 1934, p. 62) were defined by the Third International Locust Conference in 1934 as "all the centres of outbreaks" (Resolution 3(d)3); and the "outbreak centre" was defined as "a station the ecological conditions of which sometimes *provoke the transformation of a species into its swarming phase* [italics mine] (phase *gregaria*)" (Resolution 3(d)4). Zolotarevsky (1934) was able to state at this time (p. 62) that "la théorie de phases . . . est à la base de notre conception actuelle des 'aires grégarigènes' . . ."; and almost identical views were expressed much later by Brédo (1945b) and Michelmore (1947).

The stress placed by Uvarov on the concept of the "vicious circle" in phase transformation, the assumption that once phase transformation has commenced it can only continue with increasing intensity, led to investigations designed to permit the separate recognition of the phases *congregans* and *dissocians*. The idea behind these investigations was that, if *congregans* and *dissocians* could be distinguished by examination of a series of specimens, "it would be an enormous practical advantage, for this would enable the entomologist to predict whether or not swarming is to be expected" (Faure, 1932, p. 299). Lean (1936) and Zolotarevsky (1938b) both claimed to have succeeded in differentiating *congregans* and *dissocians* in *Locusta migratoria migratorioides* on the basis of structure and color [pp. 369, 371, 372], although their results were in conflict, and of uncertain significance. Du Plessis (1939) also proposed a basis for separating *congregans* and *dissocians* in *Locustana pardalina*. Other authors (e.g., Lea and Webb, 1939) failed to find any reliable differences between *congregans* and *dissocians*. Roonwal (1945) put forward three hypotheses for predicting swarming in *Schistocerca gregaria*, based upon an analysis of the percentages of forms with six and seven eye-stripes among the males and females of non-swarming populations. All of these attempts to distinguish between the two categories of the phase *transiens*, whether they were successful or not, depended for their main significance upon the assumption that an observed trend in phase transformation would necessarily be maintained in the same direction.

Uvarov's views on phase transformation and locust epidemiology were not accepted by all locust biologists. Thus Olsuf'ev (1930), while accepting the transformation of locusts (*Locusta migratoria migratoria*) into the gregarious phase under the influence of crowding, regarded this as simply a result of the increase in numbers, and not a factor constituting the actual cause of the periodicity. Tarbinskiĭ (1932), who was primarily concerned with *Dociostaurus maroccanus*, expressed closely similar views.

A number of other authors who adopted Uvarov's point of view nevertheless brought forward observations and conclusions which were, in one way or another, at variance with it. Thus Zolotarevsky (1938a) concluded (p. 262): "L'apparition des insectes de la phase grégaire sur une station ne signifie pas encore le début d'une invasion massive." Elsewhere the same author (Zolotarevsky, 1938b), referring to the occurrence of the phase *gregaria* of *Locusta migratoria* under "des conditions particulières" in certain oases in Tchad, suggests (p. 137) that "les bandes n'atteignent pas une importance qui entrainerait des migrations." In these cases transformation into the gregarious phase did not result in outbreaks. Jannone (1938) suggested that in *Dociostaurus maroccanus* the periodicity of outbreaks may be due both directly to the transformation of phase, and indirectly to meteorological and other factors affecting density.

Du Plessis (1939) reported that at a time of active incipient swarming by *Locustana pardalina*, "cases of dissociation of hopper bands were also commonly observed" (p. 10), for which the hot, dry weather and a gradual desiccation of the vegetation were held to be responsible. Zolotarevsky (1938b) had also (p. 213) envisaged the possibility that a population of the phase *congregans* of *Locusta migratoria migratorioides* might be submitted to dissociation before it could reach the phase *gregaria*, and on p. 224 he suggested that a high humidity, by reducing activity and the interattraction of individuals, might have a dissociating effect upon gregarious bands. Smit (1939), working on *Locustana pardalina*, also found (p. 102) that the supervention of environmental conditions depressing activity may reverse an original trend of transformation from *solitaria* to *gregaria*. Lea and Webb (1939), discussing the difficulty of applying the terms *congregans* and *dissocians* to ph. *transiens* hoppers of *Nomadacris septemfasciata*, pointed out (p. 26) that in 1936 small hopper bands first dissociated during the early instars, and later, in the final instar, congregated again. Kennedy (1939)

referred to the fact that the environment of the outbreak center of *Schistocerca gregaria*, while favorable to the initial stages of gregarization, brings about dissociation of any incipient bands that do not succeed in breaking out of it. Volkonsky (1941) quoted a case from North Africa in which a considerable degree of gregarization of *Schistocerca gregaria* in 1939 was completely neutralized through mortality induced by climatic factors in 1940, so that the population was pushed back into the phase *solitaria*.

It should perhaps be emphasized that in this fourth section of the account of the history of the Phase Theory we have not been concerned with the views of authors on the general phenomenon of outbreaks, but only with the relation of the phases to the development and periodicity of outbreaks. For this reason the role of multiplication has not been mentioned, although it was dealt with in the preceding section. Multiplication has certainly been accorded an important role by all workers, but the prevailing view has been that its effects are exercised through the resulting phase transformation, without which multiplication would not lead to outbreaks.

DISCUSSION OF CONCEPTS

"*Phase*"

We have seen how the term "phase" was introduced by Uvarov to designate an "infra-specific category" of a particular kind. It was to designate the "type" of the insect with reference to a continuous range of possible types produced by different levels of gregariousness (including zero gregariousness). The term "type" has to be construed in the broadest sense to include both physical and biological characters. The physical characters were the first to attract attention, and because of their permanence in preserved material have always been accorded considerable significance, but the biological characters are generally regarded as the more fundamental, and also of the greatest practical importance.

It is particularly important to note that the term "phase" was originally used, *not* for the level of gregariousness itself, nor to designate individuals exhibiting a particular level of gregariousness, but for the "type" of individual, in the wide sense indicated above, characteristic of populations possessing a particular level of gregariousness. This statement can be amply supported by a perusal of the quotations already given from the earlier papers of Uvarov, Zolotarevsky, and especially Faure [p. 367]. Thus the concept of "phase" is closely analogous in its structure to that of "ecotype" (more accurately, "ecophenotype"), although the phenomena themselves are quite distinct. "Ecotype" is used to designate, not the individuals of a plant (or animal) species occupying a particular habitat, but the "type" of individual (usually recognized by its physical characters) characteristic of populations occupying that habitat. Similarly "sun leaves" and "shade leaves" are not leaves normally exposed to the sun or shielded from it, but the types of leaves normally found in such situations, and distinguished by their form and structure. As a consequence of these features of the definition of "phase," it follows that, once the type of insect appropriate to the various levels of gregariousness has been determined, the phase of any individual can be established by a study of its individual characteristics, *quite irrespective of the degree of gregariousness it happens to be exhibiting at the time.* Moreover, if there is any conflict between the indications given by the character of the individual on the one hand, and its present level of gregariousness on the other, the character of the individual must always be the decisive consideration, since phase is defined as the type of individual *characteristic* of a particular level of gregariousness, and not as an individual exhibiting a particular level of gregariousness at a given moment.

While these implications of the definition of "phase" have in general been accepted by workers on phases, this has not been invariably the case. Thus Kennedy (1939), when confronted with a "fully gregarious swarm" of individuals with the recognized characteristics of ph. *solitaria*, could not bring himself to call this simply a swarm of *solitaria*, but contended instead that biometric characters are unsafe criteria of phase [p. 373]: see also Husain, Lahore, and Mathur (1944) [p. 377].

After it had been demonstrated that the phase differences between individuals from swarms and non-swarming populations are due to differences in population density, the phase concept tended to be linked with population density rather than with gregariousness, and we find Rubtzov (1935), Chopard (1935), Klingstedt (1939), and others [pp. 368–368–369, 369, 374] referring to phase phenomena in non-gregarious insects subject to marked fluctua-

tions of population density. When, further, it was concluded that activity is the significant factor in crowding, Faure (1943b) expressed a doubt as to whether one could properly speak of phases in *Spodoptera abyssinia*, because this factor could not be demonstrated [p. 377]. Finally Zolotarevsky (1946) defined phases as variations due to different levels of "interaction" (presumably *behavior* interaction) between individuals [p. 378].

The increasing importance attached to the biological differences between the phases, as distinct from their physical differences, was carried to its extreme by Zolotarevsky (1946), when he maintained that even a complete absence of "morphological" (presumably including color) differentiation does not necessarily signify an absence of phase phenomena [p. 378]. When this attitude is contrasted with that of Faure, for whom morphological differences, color differences, or both, were essential to the phase concept [pp. 367, 376], we are led to wonder whether there is anything really specific to the Phase Theory apart from the physical aspect. This question will be taken up again later [pp. 400 et seq.].

The Phases "Solitaria", "Gregaria," and "Transiens"

The concept of phase as the type of individual produced at a given level of gregariousness implies that there can be as many distinct types or phases as there are levels of gregariousness. A complete gradation of types extends from the one extreme of complete isolation to the other extreme of intense gregariousness. However, for practical purposes it was desirable to distinguish the types associated with sparse populations that could have had no immediate swarming antecedents from those associated with well-developed swarms. Uvarov and Zolotarevsky (1929) have proposed that this should be done by the use of the terms "*phasis solitaria*," "*phasis gregaria*," and "*phasis transiens*" [p. 366]. "*Phasis solitaria*" was to be applied to "the extreme form" represented by isolated individuals with no immediate swarming antecedents, and "*phasis gregaria*" to "the extreme form found in dense, large, emigrating swarms."

It may be noted, in passing, how these definitions, with their use of the term "form," and the latinized and italicized names for the phases, support the interpretation of the concept of phase set out above. Less formal general terms were in vogue before 1929, e.g., solitary phase, dispersed phase; gregarious phase, swarming or swarm phase, migratory phase. Some of these continued to be used after the publication of Uvarov and Zolotarevsky's paper, particularly "solitary phase" and "gregarious phase," and Michelmore (1947) even introduced the inappropriate expression "grasshopper phase."

It is obvious that the expression "extreme form" used in the definitions of Uvarov and Zolotarevsky cannot be taken literally. Strictly speaking, the extreme form in either direction would be represented by a single specimen. Of course nobody adopted this interpretation, but the stress upon extremes interfered for some time with the clear recognition that not only the ph. *transiens*, but also ph. *solitaria* and ph. *gregaria* include a range of types, and that a definition of these ranges, no doubt to some extent arbitrary, is required before the terms *solitaria*, *gregaria*, and *transiens* can be given any very definite signification. Lack of clarity on these points is responsible, for example, for the difficulties into which Faure (1932) and du Plessis (1939) were led in attempting to determine the phase of their field and laboratory material [pp. 367, 373].

The formal establishment of the three phase categories resulted in a particular connotation of the term "phase," so that "*a* phase" came to mean one of the three categories, and assigning an individual to its phase meant placing it in one of the phases *solitaria*, *gregaria*, or *transiens*.

It can be seen at once, from the accepted definition of "phase *gregaria*," that that phase cannot occur in any insect that does not, at some time or other, form "dense, large, emigrating swarms." By definition, therefore, a "grasshopper" cannot possess a phase *gregaria*, although it can show phase variation. Moreover, it would not be justifiable to survey the range of types of an insect produced by cage rearing at different population densities and to assign the term *gregaria* to that part of the range corresponding to very crowded conditions, as has been done by Rubtzov (1935) and by Faure (1943a, 1943b) [pp. 369, 376]. Yet Rubtzov's use of terms was endorsed by the International Locust Conference of 1936 [p. 370], the terminological inconsistency having apparently escaped notice. One could, of course, entertain a redefinition of the phase terms to allow "ph. *gregaria*" to be applied to the types that characterize the densest populations of any species showing phase variation, but such a redefinition has never been proposed, and

would very probably create more difficulties than it would solve. On the other hand, it is my opinion that the requirements for ph. *gregaria* might well be somewhat relaxed, and that it might be defined in more general terms as the type characteristic of swarms, i.e., of populations showing clearly marked gregariousness. This would allow the use of the term in the case of the so-called "gregarious grasshoppers." The adoption of this definition would not affect the limits of the phases in locusts, because it could justifiably be maintained that in them the type of individual characteristic of swarms is that found in the dense migrating swarms, rather than in loose incipient swarms, which latter are normally only transient formations destined shortly either to break up or to become dense and migratory. In the case of grasshoppers that do not form swarms, but nevertheless show some degree of gregariousness, with associated phase change, the term "*transiens*" might appropriately be used for the phase of the slightly gregarious individuals. Such individuals conform to the definition given by Uvarov and Zolotarevsky of ph. *transiens* [p. 366], except that they are transitional to a hypothetical, rather than an actual, ph. *gregaria*.

The formal distinction made by Uvarov (1928) between "locust" and "grasshopper," chiefly on the basis of the absence of gregariousness in the latter, has done little to promote clear thinking on the subject of the injurious Acrididae. In the same publication in which the distinction was made, the author admitted that no hard and fast line can be drawn between the two categories: that some grasshoppers are sometimes gregarious, and that all locusts behave like grasshoppers when in the solitary phase. Whatever value the distinction may have depends upon the possibility of describing a given species of acridid as either a locust or a grasshopper, however arbitrary such a classification may be in particular border-line species; but certain authors have confused this classification of species with the distinction between the phases, and have spoken of the solitary phase of a locust as a "grasshopper," or as the "grasshopper phase". Further, the restricted connotation of both "locust" and "grasshopper" has left us with no common term to use on the the numerous occasions when we wish to make a general statement applicable to both groups, and we are forced to employ the clumsy expression "locusts and grasshoppers," or the technical term "Acrididae." In the same way the introduction of the term "band" for a swarm of hoppers, and the restriction of "swarm" to the flying stage (Uvarov, 1928) has left us with no general term for gregarious aggregations of either stage. This sacrifice has been made to very little purpose, since it is usual for authors to employ redundant constructions such as "hopper band" and "swarm of adults" whenever it is necessary to avoid misunderstanding as to the stage involved. It would have been better to have retained "swarm" as a general term, and to have qualified it when necessary with the words "hopper," and "adult" or "winged."

The "Phases" "Congregans" and "Dissocians"

According to Uvarov and Zolotarevsky (1929), the term "phasis *transiens*" is "to be applied to the form occurring in a given locality when the species is on the increase and its individuals are beginning to form loose aggregations, or on the decrease, and the swarms are becoming loose and tend to scatter. . . ." This term should be replaced by "ph. *congregans*" or "ph. *dissocians*" when the direction of change is known. Moreover, observations by the junior author (Zolotarevsky, 1929) had tended to show that *congregans* and *dissocians* could be distinguished by minor details of morphology and coloration [pp. 366, 367].

Now in the terms "phase *congregans*" and "phase *dissocians*," "phase" is being used in a new sense. The term was introduced to designate types of individual characteristic of different levels of gregariousness, but "*congregans*" and "*dissocians*" could have the same level of gregariousness, and differ only in the *direction of change*. Further, the possibility of differentiating between individuals of "*congregans*" and "*dissocians*" is crucial to the question of whether these categories should be called phases, and not merely incidental, as is suggested by Uvarov and Zolotarevsky's wording. As a matter of fact, this possibility is still to some extent in doubt, even for the species with which Zolotarevsky was chiefly concerned [pp. 371, 372, 382], and the terms *congregans* and *dissocians* have been freely used by a number of authors who have claimed that no differences can be detected between them. Thus whatever terms may be used to distinguish "congregating" from "dissociating" individuals, these categories cannot be called "phases" without introducing an undesirable ambiguity into our terminology. The actual terms "*congregans*" and "*dissocians*" could, of course, be retained, and could be used in association with the term "phase *transiens*" in the form "ph. *transiens* (*congregans*)" [not "ph. (*transiens*) *congregans*"], provided it were clearly realized that "*congregans*" and "*dissocians*" represent a supplementary description of the material on the basis of direction of change, and are not themselves phase terms. How-

ever, the readiness with which phase transformation in either direction can be arrested and reversed [p. 382] is an argument against the use of any formal terms to distinguish individuals subject to one or other of these processes.

The "Phase Status" of a Population

From the definition of "phase," and particularly from the fact that phases are to be recognized by color pattern and bodily proportions among other things, it must be clear that "phase" is primarily a property of individuals. A population cannot, strictly speaking, have a phase; it can have size (number of component individuals), areal extent, and other properties, but it cannot have a color pattern or bodily proportions. However, where "phase" is used, in the narrower sense [p. 384], to mean one of the categories *solitaria*, *gregaria*, or *transiens*, it could be applied with little or no ambiguity to a population that is *homogeneous for the phase in question*, but not to one in which even a single individual belongs to a different phase. Unfortunately this point has not been appreciated by all authors, and the term "phase" has, in fact, been widely applied to populations heterogeneous in varying degree. The confusion of concepts is seen most clearly where a population is referred to the phase *transiens*. Thus Zolotarevsky (1938b) has classified certain adult populations of *Locusta migratoria* as "*transiens*" on the basis of the level of gregariousness exhibited by the hoppers from which they developed. When the individuals comprising samples of these populations were examined, it was found that the majority had to be referred either to the ph. *solitaria* or to the ph. *gregaria*, and that comparatively few actually possessed the distinctive characters of the ph. *transiens* [pp. 371–372]. Similarly, Smit (1939) applied the term "*transiens*" to populations containing numerous *gregaria* individuals [p. 374].

Notwithstanding these difficulties, we cannot do without a measure of what we may call the "phase status" of populations (as distinct from the phases of individuals), for it is with populations rather than individuals that both the ecologist and the practical entomologist are concerned. Moreover, statistical considerations preclude a reliance upon individuals in phase studies. It is essential, however, that our measures of "phase status" should be based upon the phase characters of the individuals composing the population, and not upon extraneous considerations, such as its level of gregariousness. A number of such measures are possible, and have in fact been used. One method, which has been applied extensively to hoppers, is to classify each individual in a sample of the population as *solitaria*, *gregaria*, or *transiens*, and then to characterize the population by the percentages of the three phases represented in it. Another method, which is applicable where phase characters susceptible of numerical representation are available (as in adults), is to determine the number of individuals in each of several small ranges of the character in question, and to present the frequency distribution in the form of a table or graph. Alternatively, the mean of the character in question may be used in conjunction with the standard deviation and the range.

Rao (1942), who is perhaps the only author to have expressed clearly the contradictions involved in the use of the term "phase" for both individuals and populations, introduced the expression "biometrical facies" to describe the phase status of populations of adult locusts [p. 376]. The term "phase status" is to be preferred to "biometrical facies," as being of more general connotation.

It may be noted that certain concomitants of phase variation are of such a nature that they can only be studied in populations. Thus the sexual dimorphism in size, which is characteristically reduced in populations of ph. *gregaria* as compared with ph. *solitaria*, requires at least two individuals, a male and a female, for its measurement, and a large number of pairs for accurate determination. Similarly, the percentage of individuals with 6 and 7 eye-stripes respectively can only be ascertained from a population. These are true attributes of the populations rather than characters of individuals, but they do not justify us in speaking of the "phase" of a population. Of the same nature are certain of the criteria developed by Zolotarevsky (1938b) for distinguishing the categories "*congregans*" and "*dissocians*" on the basis of the different rates of change of different morphometric ratios, and of the same ratio in the two sexes, in the course of phase transformation [p. 372].

The Physical and Biological Characters of Phases and their Interrelations

In our discussion so far, we have treated the "type" of an individual, constituting its phase, as though this were characterized by a consistent combination of different physical and biological characters such as occurs in a species or subspecies,

although we have recognized, of course, that no sharp line can be drawn between the successive phases of the sequence *solitaria, transiens, gregaria.* Much the same assumption appears to have been made by the early workers on phases. From 1932 onwards, however, an increasing amount of evidence has been brought forward to show that the correlation between the different characters of any one phase is by no means as close as was supposed.

The characters in which the phases differ may be classified as behavioral, physiological, morphological, and color characters. The more important of those that have been reported for various species are as follows:

Behavior characters: degree of gregariousness, depending upon the degree of development of the visual compensation reaction; degree of excitability; degree of activity (this is not an independent character, but is the result of the interaction of gregariousness, excitability, and, under certain circumstances, pigmentation); frequency and extent of migration; and the relative importance of visual and olfactory stimuli in controlling behavior.

Physiological characters: basal metabolism; biochemical characters, including uric acid, fat, lactic acid, and water contents, the pH of the blood, the development of melanin and acridioxanthine, and the retention of carotenoids; the temperature threshold for hatching of the eggs; the physiology of vision in relation to the histology of the eyes; thickness of the cuticle; specific gravity; fecundity; duration of nymphal development; number of instars; and food consumption.

Morphological characters: absolute size; sexual dimorphism in size; bodily proportions of the adult, as measured by the morphometric ratios E/F, P/C, H/C, M/C, E/S (S = width of sternum), E/D (D = height of eye), and C/O (O = width of head at the level of the eye); and number of antennal segments.

Color characters: nymphal color pattern; various minor features of adult coloration; the nature of the color changes associated with ageing and sexual maturation; and the number of eye-stripes.

The early authors on phases used the expression "*biometric* ratio," and this is still the one most generally employed. Pasquier (1934) and certain other French authors have used "*morphometric*," and Jannone (1938) introduced "*somatometric*." Zolotarevsky (1939) commended Jannone's term on the ground that we are concerned only with structural, non-heritable characters. The term "biometric" is clearly ambiguous, since it could refer to measurements of any biological character, including coloration, although, as used by phase workers, it is intended to exclude such characters. It is further rendered unsuitable by its extensive use as a virtual synonym of "statistical." On the other hand, "somatometric" does not restrict the reference to non-heritable characters as Zolotarevsky imagined, but to characters of the soma as distinct from characters of the germ-cells. Needless to say, the characters of the soma are controlled by both genetic and environmental factors. (In point of fact, it is quite impossible to measure, directly, any "non-heritable" character. One can only measure properties of the organism as it stands, although, if proper precautions are taken, it is possible to infer from the measurements the contribution of genetic and non-genetic causal factors.) Further, "somatometric" does not contrast the bodily proportions with color or physiological characters any more than "biometric" does. The only precise term is "morphometric," which signifies measurement of morphological (i.e., external, structural) features. This term is already in use in English-language publications on physical anthropology and vertebrate taxonomy (cf. Schaefer, 1948).

Not all of these characters are involved in phase change in any one species, and indeed some of them are affected in only one or a few species. Occasionally phase change has opposite effects on a character in two different species. Thus nymphal development takes longer in the phase *gregaria* of *Locustana pardalina* (Smit, 1939), and in the phase *solitaria* of *Schistocerca gregaria* (Chauvin, 1941) [pp. 374, 375]. On the other hand, certain characters are involved in phase change in almost every species subject to it, and are always affected in the same way. These characters are, moreover, usually the ones affected to the greatest relative extent, and may be regarded as the phase characters *par excellence.* They include degree of gregariousness, degree of excitability, the E/F ratio, absolute size (at any rate in the male), the sexual dimorphism in size, nymphal pattern, and the tendency to a general yellowing of the body, with a parallel reduction of pattern contrast, in sexually mature males of the phase *gregaria.* Nevertheless the correlation between the degrees of development of even these characters, in different populations of any one species showing a similar level of gregariousness, is so low that Rao (1942) was led to conclude that "variations in the different charac-

ters do not appear to be linked together, but occur independently" [p. 376].

To illustrate this lack of consistent correlation, we may draw together the findings of a number of authors already quoted in discussing the historical development of the Phase Theory. With regard to the behavior characters, we note that a high level of gregariousness does not necessarily lead to migration [p. 382], while migration of individual adults over distances nearly as great as those covered by swarms [p. 375], or even over much greater distances [p. 374], has been shown to occur frequently in two species, and may be suspected in others. The morphological characters are not at all closely correlated with each other: numerous authors have found a poor correlation between E/F and the pronotal ratios [pp. 367, 372, 373, 378], and between E/F and absolute size or sexual dimorphism [pp. 373, 378]. Vayssière and Lepesme (1939), in particular, found that a value for E/F typical of ph. *solitaria* could be combined in the same insect with values for the pronotal ratios that were almost typical of ph. *gregaria* [p. 373]; and Lean (1936) showed that in *Locusta migratoria migratorioides* increase in E/F within a series of *transiens* or *gregaria* was at first accompanied by an increase in absolute size, but that after a certain point further increase was correlated with a decrease in size [p. 369]. When we compare the coloration of adults with their morphological characters, we find that sexually mature adults of *Schistocerca gregaria* with morphometric ratios typical of the phase *solitaria* may show the yellow color typical of the phase *gregaria* if they occur in a swarm or are crowded in the laboratory [pp. 371, 373]. Conversely, adults developed in a swarm, and with the morphometric ratios of ph. *gregaria*, will not become yellow if they become isolated from the swarm well before sexual maturity [p. 376]. Similarly the complicated color changes associated with degree of gregariousness in adult *Nomadacris septemfasciata* occur quite independently of the morphometric ratios [p. 371]. The correlation between the color pattern of the nymphs and the morphological characters of the resulting adults is also unreliable, even when there is no appreciable change in density or degree of gregariousness between the nymphal and adult stages. The nymphal pattern is more sensitive to changes in the level of gregariousness than is the adult morphology, so that hoppers described as ph. *gregaria* can give rise to adults with morphological characters of a type normally associated with the phase *transiens* [pp. 367, 373, 374]. Isolated hoppers in which the "*gregaria*" pattern is produced by artificial means give rise normally to adults with the morphological characters of the phase *solitaria* [pp. 370, 374], and conversely isolated hoppers reared at 40°C., which have retained the coloration of the phase *solitaria*, produce adults with the morphological characters ascribed to ph. *transiens* [p. 377]. Typical "*solitaria*" nymphs can give rise to adults with "*gregaria*" coloration and morphometric ratios [p. 375]. Chauvin (1941, p. 254) has stated that there is no correlation between his "grégarisme larvaire," "imaginal," and "sexuel."

The most serious cases of inconsistent correlation are naturally those between the behavior characters, particularly the degree of gregariousness, on the one hand, and the morphological and color characters, on the other; for a lack of correlation here affects the whole of the elaborate system that has been built up for using the physical phase characters as a means of inferring the behavior of populations. It must be conceded at once that there can be no question about the *general* correlation, which has been proved conclusively for all species showing phase variation. But the discrepancies in particular cases are so frequent and so striking as to merit the most careful consideration.

Large, dense, migrating swarms of adults do not always possess the morphological characters normally associated with this level of gregariousness. Faure (1932) excluded a number of such swarms from the material on which he based his characterization of the phase *gregaria* in *Locustana pardalina* because their constituent individuals were found to be of the "*transiens* type" [p. 367]. Other "compact swarms" have been found to consist of "a mixture of *solitaria*, *gregaria*, and transitional forms" [p. 371], and a "fully gregarious" (though small) migrating swarm, morphologically "*solitaria*," has been reported by Kennedy (1939) [pp. 371, 373]. Other authors have referred to the way in which populations with "*solitaria*" morphological or color characters are occasionally observed to congregate and behave gregariously [pp. 371, 378], although they certainly do not produce large migrating swarms.

More numerous are the instances in which isolated individuals, which could certainly have had no immediate swarming antecedents, are found to show the morphological characters normally ascribed to the phase *transiens*, or even *gregaria*. Hot, dry conditions appear to be responsible [pp. 367–368,

371, 373, 377, 380]. Similarly, in rearing experiments, the color pattern of ph. *transiens* or ph. *gregaria* has been produced in hoppers kept completely isolated under conditions of high temperature, low humidity, and a poor food supply, or even under apparently favorable conditions [pp. 374, 375]. Typical phase *gregaria* adults may become detached from swarms, in which case they may revert to the type of behavior characteristic of the phase *solitaria*, while retaining their *gregaria* morphology [pp. 371, 377].

A similar lack of correlation is found if we study the morphological and color characters in relation to migratory behavior. Individuals with the physical characters of ph. *gregaria* are not necessarily migratory [pp. 371, 382], while those with the physical characters of ph. *solitaria* may on occasion undertake extensive migrations [pp. 371, 371, 374, 374–375, 375, 376, 376].

The position as regards the correlation between physical characters and behavior has been aptly summed up by Bodenheimer (1944) in the passage already quoted [p. 377], in which he has stated that neither the morphological nor the chromatic characters permit inferences as to behavior. It was this lack of correlation that led Lea (1938) to introduce the purely behavioral classification into "solitary-living" and swarming individuals, a classification which thus became contrasted with the primarily physical classification into "phase *solitaria*" and "phase *gregaria*" [p. 371].

The lack of correlation, both between the physical characters themselves, and between these and the behavior characters, especially the degree of gregariousness, is probably due to a considerable extent to the fact that the various characters are affected in what approximates to a definite sequence as the degree of gragariousness increases. Thus some degree of mutual habituation, constituting the beginnings of gregariousness, appears to precede any great increase in activity, and the latter is followed in turn by some of the physiological changes, the color changes, and the morphological changes. Among the morphological changes, the E/F ratio seems to be affected before the pronotal ratios. However, this explanation does little to help us in the problem of recognizing a "type" of individual to which, for example, the term "phase *gregaria*" would apply, because the level of gregariousness represented by "large, dense, migrating swarms" may be reached long before the sequence of changes in the physical characters has been completed, so that one character may already have reached the level characteristic of "*gregaria*," while another is still at the "*transiens*" or "*solitaria*" stage. Moreover, a considerable part of the lack of correlation is not to be explained on the basis of a time lag at all—for example, that resulting from the effects of moist and dry conditions on the development of isolated individuals, or from marked changes in the degree of gregariousness during development.

Attempts have been made to remove some of the difficulties by correlating the physical characters of adults, not with their level of gregariousness at the time, but with the level of gregariousness of the hoppers that gave rise to them: in effect, with their "history of gregariousness." But this only gives rise to fresh difficulties. Although the morphological characters of an adult are conditioned in the hopper stage, its color is chiefly the result of factors operating within the adult stage. Similarly, the black color of newly-hatched *gregaria* nymphs may be referred to their history of gregariousness (parental gregariousness), but their pattern by the third instar is a function of their degree of gregariousness within the hopper stage as well.

The inevitable result of the existence of poorly-correlated criteria, all of which have a claim to consideration in the recognition of phases, is widespread uncertainty and confusion. Thus when Volkonsky (1938) found morphometrically "*solitaria*" adults developing the "*gregaria*" coloration he spoke of a change of phase, as did Brédo (1945a) when he found morphometrically "*gregaria*" adults assuming the "*solitaria*" coloration and behavior; on the other hand, Lea (1938), faced with the same situation as Brédo, spoke of solitary-living phase *gregaria*. Kennedy (1939) was unable to regard his "fully-gregarious swarm" with "*solitaria*" morphology as anything but phase "*gregaria*," although if the same specimens had been encountered in dispersed formation they would undoubtedly have been classed as "*solitaria*."

Chauvin's terminology (1941), involving different categories of "grégarisme" [pp. 375, 381], may be briefly mentioned here. He used this term somewhat ambiguously for *manifestations* of the phase *gregaria*, and also for the *capacity* ("fait," "faculté," p. 248) to show the characters of that phase. A further ambiguity, as we have already seen, arises from the fact that the word "grégarisme" normally means "gregariousness," and thus denotes a purely behavioral characteristic. This ambiguity could be

avoided in English by anglicizing the French term to "gregarism" and using this in contrast to "gregariousness," but it is doubtful whether the term is warranted at all. The terms "grégarisme larvaire," "imaginal," "sexuel," and "résiduel" do not describe distinct *gregaria* characters so much as distinct mechanisms whereby either the same or different characters may be produced, and for this purpose the terms are poorly chosen. Thus "grégarisme larvaire," "sexuel," and "résiduel" are all estimated by the nymphal pigmentation, whose character is the same in all three; "grégarisme sexuel," no less than "imaginal," is nevertheless regarded as a property of the adult locust; finally, "grégarisme imaginal" is dependent upon sexual maturation, while "grégarisme sexuel" can be affected by stimulation received during the nymphal, i.e., pre-sexual, period. Whatever value this classification might have for purely physiological purposes, it can be of no assistance in characterizing the phases, and is, in fact, only confusing. Chauvin himself based his determination of phases purely on the pigmentation of the nymphs.

The Characterization of the Phases by Ranges of One or More Characters

In spite of its unreliability in particular cases, there is unquestionably, as we have already noted, a general correlation between the phase characters, and in particular between the level of gregariousness and the other characters. That is to say, there is no question, for example, that the individuals composing large dense swarms tend in general to approximate to the type designated phase *gregaria*. For the purpose of characterizing the three main phases, special attention has been given to the morphological characters, because these are permanent in preserved specimens, and are susceptible of numerical representation. Moreover, so far as valid comparisons can be made, it appears that the morphological characters are as closely correlated with degree of gregariousness as any of the others. The characters chiefly used have been absolute size, sexual dimorphism in tegmen length, the E/F ratio, and the ratios between dimensions of the pronotum and the width of the head. Of all these, the one most extensively employed has been E/F.

In the discussion that follows, the methods used in arriving at this characterization will be examined, and for this purpose we may take E/F as being typical of the various characters used.

Any series of specimens drawn from a population exhibiting a given level of gregariousness will show a variation in E/F. This variation may be ascribed to different causes. Individuals may be more or less responsive to identical levels of gregariousness on account of genetic differences, or of chance differences in vigor or some other character due to their individual environmental history. Alternatively, particular individuals may have been shielded to a greater or less degree from the full impact of the gregariousness of the population as a whole by some chance circumstance, or they may have been submitted simultaneously to other environmental forces which either partly neutralized or reinforced the effect of gregariousness. Further, in spite of all precautions, the series may include specimens which do not properly belong to the population at all, but to some other population exhibiting a very different level of gregariousness.

The best measure of the effect of the level of gregariousness being studied will be the mean value of the character in question, i.e., in the example we have selected, E/F. The extent of the variation within the series, or its "spread," will be given by the standard deviation, and the reliability of the mean by its standard error. These measures are essential if we are to be in a position, in the one case, to determine the chance that an individual with any given value for E/F can be a member of the population sampled; and, in the other, whether another series with a slightly different mean E/F can be regarded as significantly different or not. Yet two successive International Locust Conferences have resolved that the "true average ratio" for a series should be calculated by a method which makes it impossible to determine the standard error, namely, by calculating the ratio of the totals of the actual measurements instead of the average of the individual ratios [p. 368]. Apart from this deficiency of the Conference method, its claim to provide the "true average ratio" cannot bear examination, although it does provide a close approximation to the true average with considerable saving of labor. For if E/F should happen to be positively correlated with absolute size, and if there is any appreciable range of absolute size in the material of the series, then the Conference average will be weighted in favor of the higher values of E/F, and will therefore be higher than the true mean. Those authors who have followed the Conferences' recommendation have sacrificed part of the value of their work, chiefly because it is impossible to determine

what significance, if any, should be attached to the differences between their series means.

If sample series are taken from a number of different populations, all at a similar level of gregariousness, but at different times and places, the series means for E/F are usually found to differ significantly, and often considerably. The differences may be ascribed to differences in the levels of factors that modify the influence of gregariousness upon the E/F ratio or that influence E/F directly, quite apart from gregariousness, and also to differences in the level of gregariousness itself that were not apparent to the observer. The variation between such series can be expressed as a range, or by calculating a general mean (mean of the series means) and the interseries variance or standard deviation.

Now in characterizing the three main phases by means of E/F we are concerned, not with three levels of gregariousness, but with three *ranges* of the degree of gregariousness [p. 384]. The phase *solitaria* is the type represented by non-swarming populations ranging from extremely sparse to moderately dense, and the work of Volkonsky (1942) and du Plessis (1939) has shown that we cannot rule out effects of mutual interaction in such populations [p. 373]. The phase *gregaria* is the type represented by large, dense, migrating swarms, or, if we accept the modification of this definition suggested on p. 382, by swarms. Even within the category "large, dense, migrating swarms" there is room for a range of size, density, migratory behavior, history of gregariousness, etc., and this is all the more true of the wider category "swarms." The phase *transiens* covers the types appropriate to a range of gregariousness extending from the first signs of the phenomenon in a non-swarming population to a level just short of what we may designate a "swarm" or a "large, dense, migrating swarm." Thus in characterizing a phase by the E/F ratio, we have to determine series means for a large number of populations representing the whole range of gregariousness appropriate to the phase in question, and the variation between these series means can be expected to be greater than that between means for populations showing apparently the same level of gregariousness. The range of variation in E/F appropriate to a given phase may then be given by the range of these series means, or by a general mean and the interseries variance.

It is essential that the populations to be studied should be selected purely on the criterion of their *degree of gregariousness*. If any other considerations, such as color or morphology, are allowed to influence the selection, we end up, not with a characterization of the phases, in terms of their definition, but merely with a correlation between two phase characters, or, still worse, with something which is, to a greater or less degree, merely a numerical statement of the basis of selection itself [pp. 366, 367, 369, 369, 373]. It is also essential that the means for the different sample series representing a given phase should not be merged into a general mean without any indication of either the range of the series means or the interseries variance. When this is done, we find ourselves in the dilemma of Faure (1932) and du Plessis (1939), who could say that a given series approaches the mean value for E/F characteristic of, say, phase *gregaria*, but never knew whether it enters the range covered by the series that contributes to that mean, i.e., whether it could actually be considered *gregaria*.

Unfortunately, as we have already seen [p. 388], the range of variation even of series means is so wide, even in some of the major locust species, that there is considerable overlap, not only between the values found for adjacent phases in the sequence *solitaria*, *transiens*, *gregaria*, but even between *solitaria* and *gregaria*. That is, it is not always possible to infer with certainty whether a given population is swarming or non-swarming on the basis of the mean morphometric character. Certain extreme values can be interpreted with confidence, but there remains a considerable range within which the interpretation will be ambiguous. In these circumstances we are faced with the alternatives of (a) abandoning any attempt at close characterization of the phases, and with it the possibility of their recognition by generally accepted, objective criteria; or (b) defining a range of series means into which the great majority of the series of a given phase will fall, and using this as a rigid definition of the phase in question, irrespective of the level of gregariousness with which it may be associated in particular cases. Both of these alternatives have their adherents among authors on the Phase Theory, although they have not been consistently followed, and all their implications do not appear to have been grasped. Kennedy (1939), Husain, Lahore, and Mathur (1944), and Bodenheimer (1944) have all, openly or by implication, adopted alternative (a). The majority of authors have followed (b), although

they show indecision when faced with insects of "*solitaria*" type behaving gregariously, or with insects with "*gregaria*" ratios living in isolation, and perhaps with no immediate swarming antecedents. Ranges of series means of E/F for each of the phases *solitaria*, *transiens*, and *gregaria* have been proposed by various authors for *Schistocerca gregaria* and several subspecies of *Locusta migratoria* [pp. 368, 369, 371, 374, 375]. In some other species, authors have been content, up to the present, to establish a rough dividing value between *solitaria* and *gregaria*.

In this discussion we have used the ratio E/F as an example of a morphometric character for the purpose of examining the problems involved in using such characters for determining phase. Actually there are not one, but several such characters, and, as we have seen, these are poorly correlated with one another, and may give contrary indications. It is therefore necessary, at any rate if we propose to follow the alternative indicated above under (b), either to select the character that shows the most consistent correlation with level of gregariousness, or else to develop an index that will combine the values of several characters in a single expression.

Several workers have approached the question of determining which of the morphometric characters gives the "best indication" of phase. There seems to be general agreement that in *Locusta migratoria*, *Schistocerca gregaria*, and *Nomadacris septemfasciata* this character is E/F, although no precise statistical study of the question has been made. On the other hand, the rigorous analysis of du Plessis (1939) has shown that in *Locustana pardalina* the best indication of phase is the sexual dimorphism ratio for tegmen length, with absolute size placed second, and E/F much inferior [p. 373]. Jannone (1938) has regarded absolute size as the best character in *Dociostaurus maroccanus*, with E/F next [p. 372]. Unpublished work of my own on the Australian species *Chortoicetes terminifera* (Walk.) and *Austroicetes cruciata* (Sauss.) has shown that in the former the best character is E/F, and in the latter absolute size. Thus the "best" characters are not the same in different species, so that a rigid definition of the phases on the basis of a single morphometric character would involve the use of different characters in different species. It may be noted that the "best indication" of phase in *Locustana pardalina* is not a phase character proper [see p. 386] and could not be used to refer individual specimens to their appropriate phase, although it could indicate the phase status of a population.

As far as the author is aware, no attempt has yet been made to evolve a single index of phase based upon a number of phase characters. Rao's "biometrical index" [p. 376] is not really an index, but a condensed list, in which the two characters used (the E/F ratio and the number of eye-stripes) have not been integrated in any way. A true single index would seem to have distinct theoretical advantages, although from the practical point of view it could involve a very much greater amount of measurement and computation than would the use of the best character alone.

The Mechanism of Phase Transformation

It will be convenient to discuss under this heading concepts and terminology relating to the "outbreak process" [p. 379] as a whole, and not merely those concerned with phase transformation itself; and in this connection we may take the formulations of Kennedy (1939), Volkonsky (1942), Bodenheimer (1944), and Zolotarevsky (1946) as representing the most significant contributions to the subject in recent years. Kennedy classified the outbreak process into three successive stages distinguished by the nature of the processes taking place in each [p. 379]. Volkonsky and Zolotarevsky put forward modified versions of this classification [p. 379], so that we now have three competing classifications in which the same terms are sometimes used in different senses. It would seem that there must always be a certain degree of arbitrariness in classifying a complex process into stages in time, and greater unanimity may be expected in relation to a scheme that represents the individual processes and their interrelations. Such a scheme, in which no new terms are introduced, is presented in outline in Fig. 1.

In that figure the linking of two processes by an arrow is to be interpreted in the sense that the first process is to a greater or less degree a precondition of the second, or at least has an important influence upon it. In general, therefore, processes linked in that way are successive in time, and the time sequence is in the main from the top of the diagram to the bottom. On the other hand the picture is complicated by mutual interaction between certain processes (shown by double arrows), and by the secondary influence of one process upon another earlier in the sequence. The

latter effect gives rise to a circuit of steadily intensifying processes, of which the best example is the crucial phenomenon of the "vicious circle" of swarm formation. The diagram owes its chief inspiration to the work of Kennedy (1939), but in-

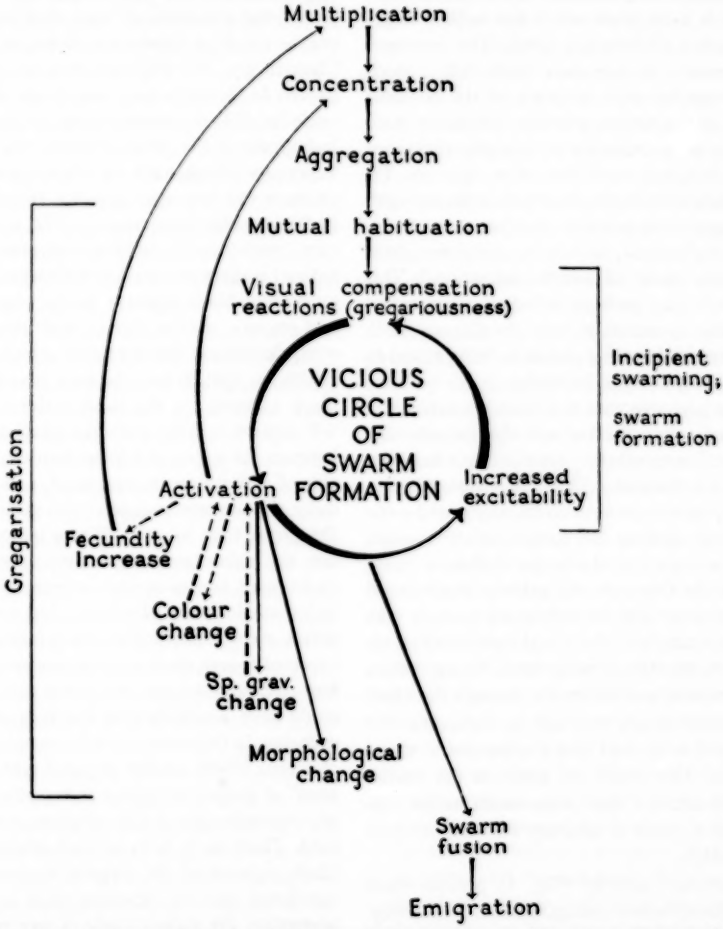

FIG. 1. DIAGRAM ILLUSTRATING THE MAJOR COMPONENT PROCESSES OF THE "OUTBREAK PROCESS," AND THEIR INTERRELATIONS

Arrows connect processes of which the first is to a greater or less degree a pre-condition of the second; broken arrows indicate a doubtful relationship. The time-sequence is in general from the top of the diagram to the bottom.

cludes certain relations that were well known before the publication of his study, and others demonstrated subsequently by Volkonsky (1942) and Bodenheimer (1944). Only the major processes and the major interactions are shown.

As has been pointed out elsewhere (Key, 1945, p. 38), the term "concentration" as used by Kennedy covers a heterogeneous group of concepts, of which "virtual concentration" and "apparent concentration" would be more properly included under "multiplication"; on the other hand "aggregation" is in its essence an intensive type of concentration, although it probably merits separate recognition in view of its special relation to gregarization. The outbreak process is thus represented (Fig. 1) as starting with multiplication (including virtual and apparent "concentration" of Kennedy), which is succeeded by concentration ("real" concentration only), and this in turn by

aggregation. Aggregation leads, as suggested by Kennedy, to mutual habituation, and a discriminative refinement and strengthening of the latent visual compensation reaction which is the root of gregariousness. At this point a marked increase in activity commences, although a less pronounced activation is to be observed in the earliest stages of aggregation (Volkonsky, 1942). The increased activity results in increased excitability, which may be regarded as a lowering of the stimulus threshold for activity, possibly by some such mechanism as a reduction of synaptic resistance following frequent repetition of a reaction. Increased excitability in turn reacts upon the strength of the visual compensation reaction so as to increase gregariousness, and by so doing completes the "vicious circle of swarm formation." This vicious circle may perhaps be better visualized as a helix rising up vertically from the diagram, each of the three participating processes being raised to ever-increasing levels of intensity.

It seems probable that the increased activity is even more closely connected with the strengthening of the visual compensation reaction than has been suggested by Kennedy. Thus the visual stimulus producing the increased activity may well be the same as that eliciting the compensation reaction, namely, movement of the image of objects across the retina. In that case the activity itself would be compensatory activity and would increase with increasing strength of the visual compensation reaction, both directly, as being the motor expression of that reaction, and indirectly through the effect of the compensation reaction in increasing the population density, and thus the amount of visual stimulation. This would not apply to the smaller increase in activity that arises much earlier, apparently as a result of olfactory stimulation (Volkonsky, 1942).

The increased activity (Fig. 1) permits more efficient concentration and aggregation (Volkonsky 1942), and thus sets up a sort of minor vicious circle subsidiary to the main one. Further, at some stage of the development of the helix, possibly as a consequence of the activation, there occurs in *Dociostaurus maroccanus* (Bodenheimer, 1944), and presumably in *Locustana pardalina* (see Smit, 1939), an increase in fecundity, which leads to a third vicious circle through its effect on multiplication. Finally, when the helix has mounted to a sufficient height, the gregariousness and activity of the swarms become sufficient to permit extensive swarm fusion, and ultimately, emigration.

In comparison with the major processes so far discussed, the classical phase changes in coloration, morphology, etc., appear in the light of mere epiphenomena, and this remains true whether we accept the conventional view that these changes are the result of increased activity, or the view of Chauvin [pp. 380–381] that they are of a "reflex" nature. In Uvarov's early conception of the vicious circle [p. 378] the development of black pigment in hoppers of the phase *gregaria* was assigned an important role through its effect upon body temperature and thus upon activity. However, neither in *Dociostaurus maroccanus* [p. 372] nor in *Chortoicetes terminifera* (unpublished observations of the author) is there any marked difference between the amount of black pigment in the phases *solitaria* and *gregaria*, yet the vicious circle remains. Moreover, developing the argument advanced by Key (1936) [p. 379], it may be seen that the effect of black pigment on the total activity of hoppers will depend entirely upon the relation that exists between the upper and lower temperature thresholds of activity on the one hand, and the average daily temperature regime of the given locality at the given time of year. Where temperatures are low, the higher body temperature of black hoppers could result in considerable increase in both the duration and intensity of activity; but where temperatures are sufficiently high, black hoppers could be expected to seek shade and become inactive well before pale hoppers, and the latter can in this way could have a considerably longer span of activity each day. In this connection the recent observations of Pielou (1948) on the dispersal and "disappearance" of gregarious groups of hoppers of *Nomadacris septemfasciata* at high temperatures are significant. There is, in fact, no real evidence that the black pigment of ph. *gregaria* hoppers plays any significant part in increasing their activity or in promoting the vicious circle of swarm formation.

Of the other phase characters, the reduced specific gravity in ph. *gregaria* has been suggested as a factor making for increased activity (Strelnikov, 1936), and other characters have from time to time been supposed to have some influence upon the vicious circle. Roonwal (1947) has presented evidence indicating that the unstriped eye characteristic of the ph. *gregaria* in *Schistocerca gregaria* is better adapted for producing sharp images of other locusts, and for use in bright sunlight, than

the striped eye of ph. *solitaria* [p. 378], so that the appearance of the unstriped eye in the course of phase transformation may promote a further development of gregariousness. However, nothing analogous to the striped and unstriped eyes of *Schistocerca* has been reported in other locusts (apart from *Anacridium aegyptium* (L.)), so that the supposed effect of this phase character cannot be of any general importance.

Altogether, it would seem that none of the classical phase characters, which preeminently distinguish the phases as "types" of individual, play an essential part, or even, perhaps, a significant part, in promoting further phase transformation. The vicious circle of swarm formation appears to be entirely a behavior phenomenon, depending upon the processes of mutual stimulation, visual compensatory activity, increase of excitability, and progressive strengthening of the visual compensation reaction. The classical phase characters are little more than pointers to the stage that has been reached in this process of behavior transformation—and unreliable pointers at that.

The "stages" of Kennedy, Volkonsky, and Zolotarevsky [pp. 379, 380] can be readily recognized in Figure 1. Kennedy's "concentration," Volkonsky's "pullulation locale," and Zolotarevsky's "pullulation" are all to be identified with the first two processes of multiplication and concentration. Kennedy's "aggregation," and Volkonsky's "agrégation" correspond to our process "aggregation." Volkonsky's "prégrégarisation" includes the processes from multiplication to aggregation or mutual habituation inclusive, while Zolotarevsky's use of the same term covers the processes aggregation and mutual habituation. Kennedy's "gregarization" extends from mutual habituation to the stage of dense swarms with ph. *gregaria* characters, while Volkonsky and Zolotarevsky employed this term for our vicious circle of swarm formation and its consequences. Further, we may recognize in the early stages of the vicious circle the "incipient swarming" of many authors, and in the vicious circle as a whole the process referred to simply as "swarm formation." There are, of course, minor inaccuracies in these correlations, due to the fact that a diagram cannot represent all the interrelations of the processes, nor the considerable degree of overlapping in time between different processes. Thus the color change in the hoppers commences while the process of aggregation is operating, although it probably does not receive its major impetus until the marked increase in activity associated with the vicious circle of swarm formation.

It may be noted that the term "gregarization," as used by all the authors cited, includes the gradual transformation of behavior and of all the other phase characters. It is thus synonymous with "transformation into the phase *gregaria*," although in "gregarization" the major emphasis seems to be placed on behavior, and in "phase transformation" on the secondary characters. The verbal form "gregarize" is a useful term, especially in such expressions as "strongly gregarized" or "weakly gregarized" individuals or populations (cf. Bodenheimer, 1944). The term "degregarization" might well be used for the reverse of gregarization, and is to be preferred to Bodenheimer's term "degregation."

Turning now to the mechanism of phase transformation in the narrower sense of the mechanism whereby the physical and physiological characters are modified, we find almost universal agreement that the changes depend upon the level of activity and excitability, usually operating through their effect upon general metabolic processes. This view is exemplified by the "locustine" theory of Faure (1932) [p. 378], and may prove to be applicable to the color changes, the physiological changes, and perhaps the changes in absolute size and sexual dimorphism. In the case of the pronotum-head ratios, Uvarov and Thomas (1941) have brought forward evidence which indicates that the changes are probably due to direct mechanical effects of the frequency of muscular contraction upon the conformation of the skeleton during development [p. 381]. A similar explanation may hold for the E/F ratio, muscular contraction being assumed to shorten the femur.

The supposed role of activity in all these effects is supported by the nature of the circumstances under which isolated individuals may develop the characteristics of the phase *gregaria* or *transiens*. Apart from the direct production of increased activity in isolated hoppers by means of mechanical contrivances [p. 380], the results of which have been criticized by Chauvin [p. 380], we know that both in the field and in the laboratory these characteristics tend to arise under conditions of high temperature, low humidity, and food scarcity [p. 380]. High temperature and food scarcity are known to stimulate activity, and the former also has a direct effect on the basal metabolism. The

apparent effect of low humidity may be due to its usual correlation in the field with high temperature and food scarcity. The effect of CO_2 in producing the *gregaria* coloration in isolated hoppers [p. 370] may be due, as hinted by Husain and Mathur (1936b), to an interference with the respiratory mechanism by means of which waste metabolites are converted into CO_2, thus leading to the same increase in their concentration that would result from their excess *production* by active crowds. Alternatively, the increase in the rate of the ventilating movements which occurs as the CO_2 tension is raised may possibly be equivalent to locomotor activity from the point of view of producing the phase *gregaria* pattern.

It must be admitted that not all those workers who have produced ph. *gregaria* characters by these various means have reported an increase of activity among the isolated insects [p. 374], and also that such characters may arise in the apparent absence of conditions liable either to stimulate activity or to produce the same metabolic effects as activity [pp. 375, 376]. However, we know too little, both about the estimation of activity and about the possibilities of reproducing its effects by other means, to evaluate the significance of these observations. Chauvin's conclusion [pp. 380, 381] that the *gregaria* coloration in nymphs and adults is the result of a nervous- and/or endocrine-controlled reaction to sensory impressions, and has nothing to do with activity, is in complete opposition to the prevailing view, and until further experiments are carried out to test this theory, the fundamental mechanism of phase transformation must be in doubt.

Phase Transformation and Outbreaks

We have seen in the historical section of this paper how the Phase Theory was, from the very beginning, linked with the phenomenon of the development of locust outbreaks, and with their periodicity, and how the transformation of the phases was regarded as fundamental to both phenomena. This crucial role of phase transformation was ascribed to its effect upon reproductive potential and migration, and to the supposed irreversibility of the outbreak process once phase transformation had commenced [pp. 364, 365, 365, 381, 381]. We have seen, also, that a few dissenting voices were raised as early as 1930 [p. 382], and that the work of a number of other investigators has to a considerable extent undermined this part of the theory, without, however, leading to open criticism of it [pp. 382, 383]. In particular, it has been shown that an increase of reproductive potential has not been demonstrated in most locusts; that extensive migrations can take place without phase transformation, i.e., in the phase *solitaria;* that transformation into typical phase *gregaria* does not always lead to outbreaks; and that phase transformation can be arrested and reversed by the operation of a number of entirely normal factors of the environment.

Uvarov (1928) has pointed out that "periodicity" is not the right term to use with reference to locust outbreaks, since there is usually no regularity about their incidence. Nevertheless the term has continued to be used, and will be retained here.

A very important circumstance that has seldom been brought into relation with the question we are now considering is the existence of outbreaks of grasshoppers, i.e., of Acrididae in which a gregarious phase is absent and migration very restricted. These outbreaks are "periodic," as in locusts, although not accompanied by sudden mass invasions. They occur from time to time over very large areas in many parts of the world. In the typical grasshopper, migration is quite insignificant, and the area within which an economic infestation occurs is identical with that in which the population increase has taken place. In other grasshoppers, such as some American and Siberian species, and the Australian *Austroicetes cruciata* (Sauss.) (Key, 1938; Andrewartha, Davidson, and Swan, 1938), a limited capacity for migration results in a narrow fringe of "invasion area" around the much larger area in which multiplication has occurred and most of the damage has been occasioned. From this condition there is a clear transition, through such species as *Calliptamus italicus*, to locusts such as *Locustana pardalina* (see Faure, 1937) and *Chortoicetes terminifera* (Key, 1945) in which areas in which multiplication has occurred (the outbreak areas) are much smaller than the invasion area, but are nevertheless of very considerable size themselves, so that damage inflicted within their confines would be a serious matter quite apart from the migrations. In *Schistocerca gregaria*, the numerous small outbreak areas are collectively very much smaller in relation to the invasion area than in the last two species, but many of them are under crops, so that significant damage can be caused within them. Finally,

in *Locusta migratoria migratorioides* and *Nomadacris septemfasciata* we have two locusts in which the outbreak areas are very few and very small, and the whole of the significant economic loss is suffered in the invasion area.

As we follow up the series from the typical grasshopper to a locust such as *Locusta*, we find that migration, from being an insignificant factor in the outbreak, becomes the crucial factor. However, we must not lose sight of the fact that the *abundance* of a pest is the distinguishing feature of an outbreak, and that migration becomes of significance only if it involves immense numbers of individuals. The most fundamental condition of an outbreak is thus an increase in numbers, and there is no evidence that the factors promoting an increase in the population of locusts in an outbreak area are different in their general character from those that lead to outbreaks of grasshoppers. Admittedly we know that in *Dociostaurus maroccanus* and *Locustana pardalina* phase transformation involves an increase in fecundity, but, on the one hand, this does not normally occur in locusts, and, on the other, no studies have been undertaken to determine whether a similar increase in fecundity may not occur in some grasshoppers at high population densities.

Thus it would seem that if any unique role is to be accorded to phase transformation in bringing about outbreaks of locusts such as *Locusta* and *Nomadacris*, it must be in relation to migration, and the demonstration that extensive migration of the phase *solitaria* can occur in several locusts is a severe blow to the theory of the relation of phases to outbreaks. It would appear that the difference in the character of the outbreaks of locusts and of grasshoppers consists primarily in the fact that the former have a capacity to migrate, rather than that they possess a gregarious phase. When the population in the outbreak areas consists of sparse *solitaria*, any migration that takes place would not be noticed; when it consists of very numerous *gregaria* it is noticed, both because of the very large numbers involved, and because their gregariousness makes the unit of observation the swarm rather than the individual (see also Williams, 1947, p. 176). Furthermore, migration at densities intermediate between very sparse and very dense must often be forestalled by the process of phase transformation, which concentrates such populations before migration commences. Thus the false impression is gained that only phase *gregaria* migrates. On the other hand, although careful comparative studies of the migration of the phases have not been made, there is evidence that transformation into the phase *gregaria* has a quantitative effect upon migration which is probably important in connection with outbreaks, at least of some species. Thus it probably makes migration more general among the locusts of an outbreak area. It also induces migration before the available food in the outbreak area is consumed, and maintains the migratory urge irrespective of the food supply in the invasion area. The evidence suggests that the phase *solitaria* migrates mainly, perhaps only, when conditions have become unfavorable.

Thus phase transformation may be regarded as a contributing factor in the production of outbreaks, at any rate of species in which migration is a condition for economic damage, but it cannot be regarded as a fundamental prerequisite, "the key to the whole problem." Furthermore, even this limited role is a function of the change in migratory behavior and fecundity only, and we have seen that the physical phase characters are not only poorly correlated with the behavior characters, but make little or no contribution to their transformation. Thus the greater the emphasis placed upon the physical characters in the concept of "phase," the less justification is there for regarding phase transformation as having a significance in the development of outbreaks.

There is even less reason to associate phase transformation of locusts with the *periodicity* of their outbreaks than with the origin of them. Even if we were to concede that the appearance of locusts in an invasion area were entirely the consequence of phase transformation, we must recognize that that transformation is itself the consequence of conditions in the outbreak areas which determine the density of the locust population there. Kennedy (1939) has concluded that the "decisive factor in an outbreak year" is multiplication ("virtual concentration") and the factors permitting it, and the same view has been expressed by Maxwell-Darling (1936) and Zolotarevsky and Murat (1938). Thus, as regards periodicity of outbreaks, locusts are in no different position from grasshoppers and many other insect pests: the periodicity is due to the periodic occurrence of particular environmental conditions.

The undue emphasis upon phase transformation as a cause of outbreaks and their periodicity

has distracted attention from the really basic causes of these phenomena, namely the multiplication of the insects as conditioned by climatic and various topographical features of the environment. Thus the outbreak area has been defined, not as a region in which conditions permit such a high degree of multiplication that swarms are formed and emigration takes place, but as a region in which phase transformation takes place (in the outbreak centres) [p. 381]. In the study of outbreak areas the emphasis has been placed upon the transformations of behavior that occur there, rather than upon the characteristics that promote multiplication. Indeed Uvarov (1937), from purely theoretical considerations connected with the environmental conditions for phase transformation, has argued (p. 6) that ". . . we can now safely dispose of the old conception that the outbreaks commence in the areas and seasons with the most favorable conditions for the species," and that the outbreak areas are actually located on the fringes of the continuous specific area, where the locust leads "a somewhat precarious existence." The same view has been expressed by Zolotarevsky (1946, p. 103).

It is difficult to see how such a view can be sustained, in view of the wealth of observations to the contrary. The outbreak areas are preeminently areas in which locusts can always be found, frequently in numbers very much above those outside. The work of Faure (1932) has made this sufficiently clear for *Locustana pardalina*, but the same observation has been made by many authors on several different species. Shortly before the commencement of an outbreak the locust population of an outbreak area is at a very high level. It is not just a matter of dense but widely-scattered local concentrations. At this stage concentration is only beginning, and a moderately dense population is spread over extensive areas (see Smit, 1939). Wherever the boundary of the outbreak area is clearly marked, for example by a soil change, the difference in the population inside and outside the area is very noticeable (see Key, 1945). It is obvious, of course, that a very low level of population is reached in an outbreak area after the emigration of swarms. It is therefore a remarkable demonstration of the special favorability of outbreak areas for multiplication that within a comparatively few years this population should be able to reach the critical density for swarm-formation once more, whereas elsewhere it remains at a comparatively low level.

Key (1945) has proved conclusively that the outbreak areas of *Chortoicetes terminifera* are located in the climatically most favorable portion of its distribution area. Within this climatic region, the limits of the outbreak areas are determined by characters of the soil and vegetation, and these, too, have been shown to be particularly favorable to the survival and multiplication of the locust (Key, 1945; Clark, 1947a).

At the risk of appearing to digress too far from the main subject under discussion, it may be of interest to consider in what way the general characteristics of locust outbreak areas could favor survival and multiplication of the insects, and why this crucial role of the outbreak areas has remained unrecognized, or has been denied, in the past.

It has, of course, been recognized that multiplication must precede phase transformation in the outbreak areas, but the general view has been that the role of these areas is to promote concentration, and that they are no more favorable to multiplication than many other parts of the permanent habitat.

Perhaps the most universal ecological characteristic of outbreak areas is a marked "patchiness" of the environment, and particularly of the herbaceous vegetation. Such a patchiness is commonly found in the ecotones between distinct major plant communities, but may also occur elsewhere. It produces a mosaic of habitats, the extremes of which may be very different. Now probably all locusts show distinct habitat preferences at different stages of their development, the preferred habitats for the eggs and for the adults, in particular, being commonly widely divergent. If we assume that these preferences correspond to differences in the favorableness of the habitats for survival and optimal functioning of each stage, it follows that a region in which the major preferred habitats are distributed in a patchwork, on such a scale that both habitats are within the normal dispersal range of the locusts, will be more favorable to survival and optimal functioning than any uniform environment. It has been observed that locusts of several species do, in fact, utilize the patchiness of their outbreak areas in their various activities (cf. Kennedy, 1939, Smit, 1939, Bodenheimer, 1944, etc.).

Apart from providing optimal habitats for differ-

ent life-cycle stages, a patchy environment of the right type has a buffering effect on gross climatic variation. In such an environment a mobile insect can find optimal, or at least tolerable, microclimates under the most extreme general climatic conditions, and its survival and normal functioning are thereby promoted. Further, in a patchy environment one extreme habitat is connected with the other extreme by a gradient of intermediate conditions. Weather and seasonal factors may alter the characteristics of an area that was formerly optimal for a given stage of the life-cycle, but at the same time these factors would be likely to reproduce the optimal habitat a little further along the gradient between the two extremes, so that in effect all that has happened is that the optimal habitat has shifted its location.

These advantages of a patchy environment from the point of view of keeping locusts alive under unfavorable conditions, and promoting their rapid increase under more favorable ones, seem evident enough. However, precisely the same patchiness is conducive, largely for the same reasons, to periodic concentration and, on the smaller scale, aggregation of locusts, and thus to phase transformation (cf. Uvarov, 1937, and others). The predominant preoccupation with phase transformation as the crucial process in the development of outbreaks, and as the criterion of outbreak areas, has had the result that the concentrating function of the patchy environment was regarded as sufficient explanation of its close association with outbreak areas, and its more fundamental function in relation to multiplication was overlooked.

Another very general characteristic of outbreak areas is climatic instability. This, also, has been evaluated almost entirely in terms of concentration, as promoting wide fluctuation in the areas of favorable habitats (cf. Uvarov, 1937), and synchronizing the life-cycle. However, this instability must have another consequence which may well be of much greater importance in locust epidemiology. In a favorable but stable natural environment an insect population tends to approach a stable equilibrium with its predators and parasites, and this precludes excessive multiplication of any one member of the system. In an unstable environment, on the other hand, the host can temporarily escape from the restrictive influence of its biotic controls and build up to very high numbers. When this is accompanied by migration, the food supply can recover, and the stage is set for a repetition of the process with the next swing of the climatic cycle.

The arid nature of the outbreak areas of many locusts has perhaps contributed to the belief that they must be relatively unfavorable. Apart from the fact that aridity is usually associated with the favorable factor of climatic instability, this view also ignores the deleterious effect of over-moist conditions upon most Acrididae. This effect seems to operate mainly through bacterial and fungal diseases, and is so powerful as to restrict certain species to regions with an annual rainfall of less than 10 in., when there appears to be no other reason why they should not occupy better country in which their food supply would be assured. The fact that a population increase of such species follows good rains in the arid regions is not necessarily relevant to the question, because there is a very great difference ecologically between occasional heavy rain in an arid region and continuous humid conditions of the same degree elsewhere.

For an elaboration of the point of view of the preceding paragraphs in relation to *Chortoicetes terminifera* and *Austroicetes cruciata*, the reader is referred to the work of Key (1945) and Clark (1947a, 1947b).

The conclusion that phase transformation, even in its purely behavioral aspects, is a subsidiary factor in locust epidemiology calls for a restriction in the use of phase terminology in this field, and such restriction is the more necessary the greater the emphasis placed upon physical characters in the definition of phase. In epidemiology the expression "phase transformation" can almost always be replaced with advantage by the expression "swarm formation." The term "swarm" includes the ideas of large numbers, gregariousness, and migratory capacity, and "swarm formation" thus describes very adequately the crucial process from the point of view of the development of a locust outbreak. It further avoids all the ambiguities of the phase terminology. From the point of view of epidemiology it is almost entirely immaterial whether the individuals composing a locust swarm are typical phase *gregaria*, or, as in the swarm described by Kennedy (1939), typical phase *solitaria*. The Fourth International Locust Conference placed the emphasis in the wrong place when it resolved [p. 370] that the phase *solitaria* is "relatively harmless," and the phase *gregaria* "dan-

gerous": it is only numbers and migratory capacity that are dangerous.

Australian workers on locust epidemiology have avoided the phase terminology altogether, and have employed such expressions as "swarm formation," "non-swarming population," etc., without any loss of meaning and without undue circumlocution. Faure (1935, pp. 27–28) has also described the origin of an outbreak quite successfully without reference to phase transformation. The author has elsewhere (Key, 1938, 1945) proposed definitions of "distribution area," "infestation area" (which includes "invasion area"), and "outbreak centre," in which the usual phase terminology of these definitions is replaced. The whole range of distributional terms used in locust ecology may be defined along these lines as follows:

Total distribution area: The region in which the species has at any time been found.

Area of permanent occupation: The region in which the species is always to be found (i.e., if searched for with sufficient thoroughness in the right habitats and at the right time of year).

Infestation area: The region in which swarms of the species have at any time been found.

Outbreak center: An area the ecological conditions of which sometimes lead to swarm-formation, and all parts of which contribute to this effect.

Outbreak area: An area containing numerous outbreak centers interspersed with non-outbreak-center country, and usually separated from the surrounding country by relatively sharp discontinuities in frequency of outbreak centers and in topographical features (including soil and vegetation, as well as physiography).

Outbreak region: The whole region in which the outbreak areas are situated.

Invasion area: The region which has at any time been invaded by swarms, but in which swarm-formation cannot occur (i.e., the infestation area less the outbreak areas).

Swarm-formation itself may be defined as "the formation of swarms from a non-swarming population."

What Does the Phase Theory State?

We may now pass from the component concepts and terminology of the Phase Theory to the Phase Theory itself. It is remarkable that the literature should contain no clear and simple statement of what the Phase Theory actually is. In spite of this lack, it is possible to infer, particularly from Uvarov's own earliest publications on the subject, what the basic propositions are. Unfortunately, the lack of clarity at the beginning has opened the door to varied interpretations and extensions of the content of the theory, so that it is by no means certain that general agreement can now be obtained on its scope.

It has already been stated [p. 364] that the theory as originally presented could be reduced to three propositions. Of these, only two are really fundamental, namely:

1. In certain locusts there are two distinct forms of infraspecific status—the "phases"—which are connected by transitional forms, and are mutually transformable in successive generations; and
2. The transformation of the phases is responsible for the periodicity of locust outbreaks.

It has been shown above that the second of these propositions cannot be upheld: that, in fact, phase transformation is at most a contributing factor in locust outbreaks, or one responsible for certain features of the outbreaks only. This leaves us with the first proposition, and we have now to consider what expansion of that proposition is necessary in the light of our increased knowledge.

In the first place, we have to decide whether we can agree with Zolotarevsky (1946, p. 43) in admitting to the field of the Phase Theory variations due to the interaction of individuals, if no physical differences between the two types can be discerned [p. 378]. This involves the question, already raised in this paper [p. 384], whether the Phase Theory can have any specific content at all if it does not concern itself primarily with physical differences. All the other phenomena of phases, as Zolotarevsky (1946) has rightly stated [p. 378], and Klingstedt (1939) and Chauvin (1941) also suggested, have been well known for many years in a wide range of animals. Migration, for example, has been studied in some detail in birds, fishes, mammals, and insects. It is commonly associated with temporary gregariousness, sexual maturation, or both. It involves extensive mutual interaction of individuals, increase of their activity, and alteration of their usual behavior patterns. Parallel with these changes go fundamental physiological changes. Incidentally, these migrations may lead to what one might call "outbreaks" of the species concerned in the region invaded. Where these changes have not been found to involve parallel "physical"

changes, or at least significant changes in the type of physical character used in the taxonomy of the group, they could be, and were, studied perfectly satisfactorily without the aid of any Phase Theory. It was only when a species was encountered in which the individuals composing gregarious populations were found to be so unlike those composing non-gregarious populations as to be regarded as a distinct species that scientific advance was blocked, and the stage was set for a theory that would reintegrate the species as an object of study, by declaring that the two forms are conspecific and mutually transformable. In investigating the epidemiology of locusts, workers who had been baffled by the apparently complete disappearance of the species after one outbreak, and its reappearance "from nowhere" at the commencement of the next, could then apply the appropriate ecological methods of study to the species over its whole range of abundance, with very gratifying results. It appears incontrovertible that, were it not for the fact of physical (morphological and color) differences between gregarious and non-gregarious populations of locusts, there would have been no Phase Theory and no need for one.

Many prominent workers on phases appear to have adopted the view that the fields of study (in ecology, epidemiology, and social behavior) that were thus made possible by the major contribution of the Phase Theory in reintegrating the species should be, so to speak, taken under the banner of the Phase Theory itself, becoming extensions and logical consequences of it. It is probably along some such lines as these that the mistaken emphasis came to be placed on phase transformation in connection with the periodicity of outbreaks. As a result the concept of the Phase Theory has steadily widened, until to many authors it calls to mind the periodicity of outbreaks, the recognition of outbreak areas, and the mechanism of the development of gregarious behavior, rather than physical differences. Zolotarevsky's references (1946, p. 108) to the mysterious "nature" of the phenomenon of phases, as distinct from their "manifestations," strike an almost metaphysical note; for if the Phase Theory is concerned with anything at all, it is concerned precisely with "manifestations." We must, then, retain the concept of physical differentiation as the core of the Phase Theory.

The Phase Theory as originally promulgated referred only to locusts. Subsequently, phases were shown to exist in other Orthoptera [pp. 368, 369, 377] and in certain Lepidoptera [pp. 376, 377, 378]. It seems very probable that at least rudimentary phase differences may be found in other groups of insects, and in animals other than insects. The theory should be stated in sufficiently general terms to cover these possibilities. Further, the original theory specified *two* distinct forms, although these were connected by a complete series of intergrades. In discussing the concept "phase," the view has been taken that this term is applicable to all the innumerable forms of the series [pp. 383, 384], so that the number of possible phases becomes infinite.

Finally, it seems essential to include in any statement of the Phase Theory a definition of the particular *kind* of variation with which the theory deals. As we have seen [pp. 383, 383], the phases were originally regarded as types of individual associated with different degrees of *gregariousness*. As investigations continued, it was found that both the physical characters of the types and their degree of gregariousness are determined by the *population density*, and that population density exerts its influence through *mutual stimulation*. *Activity* has long been regarded as the usual means whereby mutual stimulation determines phase, although this has been denied by Chauvin (1941). We cannot be content with Zolotarevsky's "interaction" as the determining factor (Zolotarevsky, 1946), because physical changes that have nothing to do with phases can result from interaction (e.g., changes in size due to competition for food, or the controlled production of castes in social insects). In view of the occurrence of physical changes, in all respects analogous to phase changes, in insects that vary strongly in population density but do not show actual gregariousness (Rubtzov, 1935; Chopard, 1935; etc.), and also in sparse, non-gregarious populations of locusts of different density (du Plessis, 1939; etc.), it appears unwise to restrict the Phase Theory to physical types associated with gregariousness. At the same time, we can hardly admit as a phase any physical type owing its character to a particular level of *activity*, quite apart from the doubts on the significance of activity introduced by Chauvin (1941). The nature of the variation we are concerned with seems to be fully specified, however, if we say that it normally depends upon *the degree of mutual stimulation in populations of different density*. The qualification "normally" is necessitated by the evidence that

more or less typical phase changes can be produced, at least in the laboratory, in isolated individuals.

CONCLUSIONS

In the light of the considerations brought forward in the above analysis, the following conclusions may be drawn:

1. Uvarov's Phase Theory, which has never been succinctly formulated, may be stated as follows:

> In certain animals, different degrees of mutual stimulation between the individuals composing populations of different densities lead to the appearance of distinct physical types—the "phases"—which typically differ also in their physiology and behavior. The phases may, within one or several generations, be transformed one into the other by an alteration in the degree of mutual stimulation.

In this statement the accent is upon physical differentiation (without which the theory could have no specific content), in relation to population density rather than gregariousness. No limit is placed upon the number of phases that may be recognized, and the scope of the theory is widened to include any animal.

2. Phase transformation must be regarded as a secondary concomitant in the development of locust outbreaks, or at most a minor contributing factor in which only certain aspects of the transformation are significant. The development of outbreaks and their periodicity are not, strictly speaking, the concern of the Phase Theory at all.

3. A phase is a type of individual whose distinctive physical and other characters are of the kind determined by the amount of mutual stimulation experienced in a population of a particular density.

[It is, of course, a simpler matter to define "phase variation" than "phase." The former is a more abstract concept, and as such can be isolated in thought from other kinds of variation to which an animal may be subject. "Phase," while still an abstraction, refers to the characters of concrete individuals in which the effects of phase variation cannot be completely separated from those of other sources of variation. Thus phase variation is superimposed upon variation due to independent environmental and genetic factors affecting the same characters, though usually to a much smaller degree. Further, the degree of mutual stimulation, and hence the extent of phase variation, may itself be modified by environmental and internal factors acting independently of population density.]

4. In a more specific sense, a phase is one of three such types designated respectively *solitaria*, *transiens*, and *gregaria*. The phase *solitaria* is the type characteristic of populations showing no trace of gregariousness, and whose immediate antecedents also showed no gregariousness. The phase *gregaria* is best defined as the type characteristic of swarms, i.e., populations showing clearly-marked gregariousness, and behaving substantially as collective units. The phase *transiens* is the type characteristic of populations with a history of gregariousness intermediate between that of *solitaria* and *gregaria*.

5. Non-gregarious grasshoppers, and other non-gregarious animals, cannot, therefore, possess a phase *gregaria*, even when they occur in dense populations; but they may show phase variation. If they show slight gregariousness, without forming definite swarms, they may be conceded a phase *transiens*.

6. The categories "*congregans*" and "*dissocians*" are not phases, because they are not defined on the basis of a difference in mutual stimulation, population density, or gregariousness, and do not necessarily display distinctive physical or other characters. If one wishes to indicate the direction of phase change, such terms as "gregarizing individuals" and "degregarizing individuals" might be used, although it is necessary to remember that there is never any guarantee that an observed trend in phase transformation will be maintained in the same direction for any length of time.

7. "Phase" is essentially a characteristic of individuals. However, a population may be said to have a phase, in the specific sense of ph. *solitaria*, *transiens*, or *gregaria*, if it is entirely homogeneous for the phase in question.

8. A measure of what may be called the "phase status" of a population may be obtained in the form of means and standard deviations for suitable phase characters of the component individuals, or by a frequency measure. In the case of a morphometric ratio, any such mean must be the mean of the individual ratios, and not the ratio of the totals of the absolute measurements, as recommended by successive International Locust Conferences. The phase status of a popu-

lation may also be estimated by the sexual dimorphism ratio and other measures which, while depending upon individual phase characters, are not themselves measurable in the individual.

9. The degree of correlation between different phase characters, both physical and biological, is low, so that the indications of phase given by different characters may be markedly conflicting. This makes it impossible, for example, to draw reliable inferences as to behavior from the physical characters, and has led to general confusion as to what is implied, in any particular instance, by the phase terminology.

10. As a consequence, we are faced with the alternatives of (a) reconciling ourselves to using the phase categories in a vague way to indicate types with ill-defined constellations of characters, or (b) defining the phases of each species in a rigid, if somewhat arbitrary manner, by means of ranges of values of the best morphometric character for differentiating the phases in that particular species. This choice is by no means an easy one, but alternative (b) is to be preferred, since it does provide a completely objective basis for defining the phases by using that physical character, open to quantitative estimation, which is the most intimately associated with the cause of phase differences. Adopting this course, it is clear that only adult insects, with the parts to be measured undamaged, can be classified into phases. Nymphs and damaged adults cannot be identified with certainty. While this is unfortunate, the situation is no different from that in which material of all stages is placed under alternative (a), where, since the phases themselves are not rigidly defined, no specimen or series can be certainly identified.

[Since the whole field of locust ecology and epidemiology can be studied without reference to phases, the phase terminology could no doubt be dispensed with altogether if we had only the requirements of this field to consider. But the phases have a taxonomic, as well as a biological significance. Taxonomy is concerned with the full range of physical variation of a species, and well-marked infraspecific forms need to be differentiated and named.]

11. In determining the ranges of the best morphometric character for use in defining each phase, the following procedure is desirable: Numerous large series of specimens should be obtained for a number of different localities and seasons, and representing the full range of gregariousness from sparse non-swarming populations with non-swarming antecedents up to the largest and densest swarms with swarming antecedents. These series should be grouped, purely on their degree and history of gregariousness, as "non-swarming with non-swarming antecedents," "swarms," and "intermediate." Series means, group means, and the interseries variance within each group should be calculated for each major morphometric character. The best indicator of phase may then be selected as that character which gives the most significant differences between the groups. This best indicator should be a phase character proper, and not, for example, the sexual dimorphism ratio, which cannot be applied to individual insects.

Using the series means of the best indicator, the range of means corresponding to each of the three categories of gregariousness should be determined. Overlap will be found, not only between the ranges for adjacent categories in the gregariousness sequence, but sometimes also between the range for non-swarming populations with non-swarming antecedents, and the range for swarms. Arbitrary limiting values should then be selected so as to give three contiguous, non-overlapping ranges, in which a maximum proportion of the series means will fall into the phase to be expected from the degree and history of gregariousness of the series. The phases in the particular species concerned are then rigidly defined by these ranges of the best indicator. The phase status of any series can then be determined as *solitaria*, *transiens*, or *gregaria* on the basis of its mean for the selected character, and any individual can be assigned to its phase on the basis of its individual value for the character.

12. It remains desirable to have some means for indicating the general phase affinities of nymphs, etc., which cannot be definitely classified under the system proposed. Sometimes it may be best simply to describe in a few words what the significant characters of such individuals are. Thus one might speak of "*black* first-instar hoppers." Something more than this is required to indicate the general ensemble of characters, and the terms "solitarioid," "gregarioid," and "transientoid" might be used for that purpose, not italicized, not accompanied by the word "phase," and necessarily of somewhat uncertain connotation. For example, one might say: "The swarm of yellow, gregarioid adults, of which no specimens were taken, produced typically gregarioid hopper progeny. Stragglers from this band became transientoid by the final instar, and

gave rise to ph. *transiens* adults." The same terminology could be used for species in which phase studies are not sufficiently advanced for rigid definition of the phases to have been possible.

13. The "outbreak process" is more readily analyzable into operative processes than into stages in time. The essential process is the "vicious circle of swarm formation," which is a purely behavior phenomenon. The classical physical phase differences arise as secondary consequences of the outbreak process, and play no important part in promoting either further phase transformation or further development of the outbreak process. They are, at most, pointers to the stage that has been reached in the outbreak process, and somewhat unreliable pointers at that.

14. The definition of the phases on the basis of physical characters, coupled with the uncertain correlation between the physical characters and behavior, calls for an independent classification of individuals and populations on a behavior basis. The unambiguous terms "swarming" and "non-swarming" are proposed for this purpose, the latter being synonymous with "solitary-living." The dual classification then permits such combinations as "swarms of ph. *solitaria*," "non-swarming gregarioid hoppers," etc.

15. The fundamental cause of outbreaks of locusts is multiplication, and the "irregular periodicity" of outbreaks is primarily due to changes in the population level of the outbreak areas, whose ecological characteristcs are particularly well adapted to permit survival under unfavorable conditions and rapid multiplication under favorable conditions. Several features of the outbreak areas that make them favorable for locust multiplication also promote concentration, and thus set in train the development of gregariousness and transformation into the ph. *gregaria*. In the course of these changes migration is probably stimulated; certainly it is made immediately obvious, and practically significant, on account of the gregariousness of the insects and their numbers.

16. The factors of abundance, gregariousness, and migratory capacity are all reflected in the word "swarm," and the essential process that goes on in the outbreak areas is best described as "swarm formation." It is the change in the abundance and behavior of locusts in the outbreak areas that produces an outbreak, rather than phase transformation. "Outbreak area," "outbreak center," and other distributional terms used in locust epidemiology are therefore best defined in terms of the contrast between swarms and non-swarming populations, rather than the contrast between the phases.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition there will occasionally appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to H. B. Glass, Associate Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *Department of Biology, The Johns Hopkins University, Baltimore 18, Maryland, U. S. A.*

THE SCIENCE OF ECOLOGY TODAY

BY TH. DOBZHANSKY

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A review of PRINCIPLES OF ANIMAL ECOLOGY.

By W. C. Allee, Alfred E. Emerson, Orlando Park, Thomas Park and Karl P. Schmidt. W. B. Saunders Co., Philadelphia and London. $14.00. xii + 837 pp.; ill. 1949.

It is no longer a common practice among biologists, as it used to be up to about a generation ago, to write books summarizing the state of knowledge in their branch of science. This is probably because, in our day of intense research activity in many fields, new data accrue so rapidly, chiefly in the form of short journal articles, that a summary becomes antiquated often before the printer's ink is dry. Yet such books are invaluable to advanced students and to beginning research workers who need to find out what has and what has not been accomplished by their predecessors in their chosen field; textbooks do not serve this purpose, except incidentally. Such books are also a boon to workers in related disciplines, who otherwise find it difficult to keep abreast of developments outside their own specialty. It is, therefore, extremely gratifying that the five most eminent representatives of the Chicago school of ecology have written "a study of the underlying principles [of animal ecology] together with a sampling of the evidence on which they are based." The "sampling" is, however, so generous, (the bibliography alone occupying 71 pages), and the presentation so concise that the book approaches the status of a full-fledged encyclopedic treatise on modern animal ecology.

It may well be that ecology has needed just such a treatise more than any other biological discipline, because it covers an exceptionally broad field with somewhat indefinite boundaries. The authors define ecology as "the science of the interrelation between living organisms and their environment, including both the physical and the biotic environments, and emphasizing interspecies as well as intraspecies relations." Ecology impinges upon almost every other biological discipline, and upon several physical sciences as well. The book under review discusses topics as diverse as geological climates, oceanic currents, atmospheric gases, soil chemistry, mutualism and parasitism, human demography, interspecific competition, the organization of insect societies, marine sediments, environmentally induced mutations, hybrid sterility, rudimentation, sexual selection, etc. This does not, however, mean that ecology has become a sort of holding company superimposed upon other disciplines; it means that ecology is a discipline in which synthesis plays a greater role than it does in many other fields, and which may accordingly be instrumental in tying together otherwise scarcely related specialties. It is therefore important to show, as this book does so admirably, how the almost bewilderingly diversified subject matter fits together with a core of clearly defined principles. And it must be noted in this connection that although the book under review claims to cover only animal ecology, the authors have, as they were well-nigh forced to, drawn freely upon plant material. Nevertheless, this reviewer cannot restrain himself from expressing a regret that botanical ecologists are not included among the authors so that the word "animal" might have been deleted from the title.

The book opens with an introduction containing important definitions and statements of principles and a concise history of ecology. This was written by W. C. Allee, Thomas Park, and K. P. Schmidt. There follows a section on the Analysis of the Environment, written mainly by W. C. Allee, which is a masterpiece of lucid presentation and of integration of most diversified material. Sections on Populations (by Thomas Park) and on The Community (by Orlando Park) form the central portion of the book, which concludes with a section on Ecology and Evolution by A. E. Emerson.

Park defines *population* as "any single or mixed species association in the laboratory or in nature that presents a closely interacting system which can be studied and expressed with some quantitative rigor." This is, of course, a much broader concept than the (Mendelian) population of geneticists, which is a group of sexually reproducing and cross-fertilizing individuals which possess a common gene pool. Ecological population studies include the analysis of natality, mortality, age distribution, rates of growth, equilibria, oscillations, and interspecies competition in populations. The *major community* is defined (by O. Park) as "a natural assemblage of organisms which, together with its habitat, has reached a survival level such that it is relatively independent of adjacent assemblages of equal rank; to this extent, given radiant energy, it is self-sustaining." In my own opinion, this very cogent definition represents a goal to be aimed at in community studies; up to now, such studies have been in the main descriptive rather than analytic, and have given little information on the survival levels and self-sustaining abilities of the assemblages examined. This should not be construed as a criticism of the definition—definitions may be more useful if they serve to direct further research into proper channels than if they merely summarize the inadequacies of the present knowledge.

The short chapter on Animal Aggregations (by W. C. Allee) is, to me, one of the most thought-provoking in the book. The central idea here is "that natural, unconscious mutualism is one of the basic principles of biology." This generalization is supported by a mass of diversified evidence which shows that the protocooperation and cooperation of organisms of the same and of different species have great survival values. This is, evidently, an important corrective to the naive view that evolution is promoted exclusively by the struggle for existence. The "struggle" involves cooperative as well as disoperative elements, and the former are adaptively more efficient. This idea is extended further by A. E. Emerson in the concluding pages of the book, where the adaptive value of the integration of organisms in communities is visualized as leading to formation of "a biotic system that may appropriately be called an interspecies supraorganism. The incorporation and control of the physical habitat by the interspecies supraorganism produces a unitary ecosystem." The validity of the concept of supraorganism will depend upon the precise meaning put into it; in my opinion, no serious objection should be raised against its use in the book under consideration, but it is a construct which is peculiarly apt to be misused if incompletely understood.

The inclusion in a treatise on ecology of a thorough account of modern theories of evolution connotes a most important development of ecological thought, one in which A. E. Emerson has been a leader. Indeed, it is the evolutionary idea that gives an internal unity to the field of ecology; and ecological investigations contribute basic data for an understanding of the mechanisms of evolution. If the book under review were to accomplish nothing more than to persuade ecologists that the above propositions are true, its important role in the history of ecology would be assured. The manner of presenting evolutionary theories adopted by Emerson resembles, among existing models, that in the well-known book by Julian Huxley. Both presentations are characterized by a profusion of references to the literature, of inestimable value to students of the subject (needless to say, Emerson has used much new literature and many sources not known to Huxley). The viewpoints of Emerson on certain controversial problems happen to differ from my own. Thus, the arguments presented in favor of the possibility of sympatric speciation do not seem convincing, and do not answer the objections against this possibility recently formulated by Ernst Mayr. The inclusion of geographic (spatial) isolation among reproductive isolating mechanisms is hardly defensible, since, as Emerson admits, geographically isolated populations may be genetically identical while reproductively isolated ones are necessarily different; furthermore, the term "reproductive isolation" has been proposed specifically to distinguish between the geographical and other forms of isolation. Failure to distinguish between these categories of isolating mechanisms leads to a lack of clarity in the species concept. Despite these, and some other disagreements, this reviewer can only endorse Emerson's general evolutionary views. It is a most gratifying fact that in our day investigators who start from such diverse fields as ecology, genetics, paleontology, systematics, or comparative and experimental morphology and embryology have arrived at concordant interpretations of the evolutionary process.

In conclusion, I quote the last sentence in the book, which epitomizes its general spirit: "Principles that assert facts in meaningful order have not fulfilled their purpose unless they stimulate further fact finding, further discovery of relationships, further synthesis, and ultimately contribute to the evolution of human wisdom."

REVIEWS AND BRIEF NOTICES

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GENERAL BIOLOGY: PHILOSOPHY AND EDUCATION

SURVEY OF BIOLOGICAL PROGRESS. *Volume I. Edited by George S. Avery, Jr. Academic Press, New York.* x + 396 pp.; ill. 1949.

Within recent years growing numbers of harassed investigators in the fields of physiology, biochemistry, or microbiology have turned with gratitude to existing literature surveys presented in the form of annual reviews. These reviews provide a partial solution to the problem of keeping informed in areas of information not strictly on the reader's high priority list for source reference. The addition of the *Survey of Biological Progress* to the ranks of such volumes will be received with interest by a more general audience than has been reached in previous attempts to compile current literature into an assimilable form for the non-specialist. Research workers compelled professionally to assume a myopic view of the scientific scene, together with teachers of the life sciences, will find these eleven review articles with their bibliographies a valuable compendium of reference material. Nevertheless, individuals will see the volume in the light of their own spheres of interest, and the wide range of subject-matter entails a risk that for some persons the "misses" will outnumber the "hits." The average reader may then look into the book for the sake of one or two articles marginal to his areas of knowledge, though a study of all will provide a beneficial antidote to overspecialization, and thereby fulfill an avowed aim of George S. Avery, the editor-in-chief, and his distinguished editorial and advisory staff.

Three papers are concerned with experimental botany. K. C. Hamner has described the role of environment in modifying the vitamin concentrations of edible plants. Techniques and points of emphasis in the cultivation and production of disease resistant plants are covered in another chapter, by W. A. Frazier. The influence of growth hormones on normal plants and the contribution of these hormones to cellular proliferation in tissue cultures, regenerative tissue, and plant tumors is well reviewed by Philip R. White, an authority whose significant contributions to the subject are widely known. Discussions of cellular adaptation and habituation of tissues on defined medium are presented without any reference to a possible contribution of genetic variability to the adaptive process, a subject of paramount interest to workers in related fields.

Another contributor, L. M. Black, departs periodically from his description of plant viruses to give salient similarities or differences in the virus tumors of the frog, fowl leucosis, Rous sarcoma, and mammary mouse cancer; and fibroma, myxoma, and infectious warts of the rabbit. Students of psychosomatic medicine claim to have shown the subsidiary importance of psychic factors in the etiology of infectious warts in humans. Let reader and rabbit rejoice that this added intangible is not yet fair game for Black and his colleagues.

A brief chapter by G. E. Hutchinson and E. S. Deevey, Jr. surveys current progress in ecology. In another section R. K. Burns has discussed critically the influence of hormones in sex differentiation. The development of successful methods for the castration of mammalian embryos in utero has given new evidence of the significance of the embryonic gonad in the establishment of sex patterns. In spite of paradoxes, some orderly relationships prevail. Response of the embryo to specific dietary deficiencies, and the more general problem of nutrition as it affects various phases of reproduction is the subject of an analysis by K. F. Mason. Martin Kamen fulfills his now traditional role as the reviewer of tracer methods in biological research. The remarkable advances recently made in the genetics of bacteria and viruses are competently surveyed by Bentley Glass in a discussion of the gene and gene action. In broader scope, his article continues with recent discoveries in chemical and physical mutagenesis, position effect, multiple allelism, and with an integretive treatment of the uncertain but challenging relationship of genes, plasmagenes, viruses, enzymes, and the meristic chemical entities governing many of the most fundamental biological processes. Glass's article forms a logical prelude to some sections of the chapter on growth and development by D. P. Costello. Harriet Creighton's thoughtful treatise on pedagogical problems in biology is of potential value to all teachers. Charles Darwin and other intellectual giants of the 19th century might take exception to her statement that "40 or 50 or even 20 or 30 years ago, a large proportion of what was known could be presented in 1 year." It is rather that our changing interests have left much of the past in obscurity. Modern biology, as represented in this book, is very much a topical and an experimental science.

VERNON BRYSON

PROTOMORPHOLOGY. *The Principles of Cell Auto-Regulation. By Royal Lee and William A. Hanson; with an Appended Article on "Cytotoxines" by K. R. Victorov. Lee Foundation for Nutritional Research, Milwaukee.* $8.50. xxviii + 365 pp.; ill. 1947.

The central theme of this book seems to be the discussion of the hypothesis that the genes contain an organized assemblage of smaller units, *cytomorphogens*, which are composed of still simpler, quite stable units composed principally of minerals which are the determinants for the specificity of the biological proteins; these basic determinants are the *protomorphogens*. The

protomorphogens are discussed as exerting profound effects on the activity of all living cells. Protomorphogens are related in this volume to organizers, to thromboplastin, to cancer, to arthritis, to senescence, to the nausea of pregnancy, to name only a few of the many entities or conditions taken up in the volume. The authors seem to associate "raw" protomorphogen with Burrows' "archusia" and protomorphogen associated with a lipoid "wrapper" with Burrows' "ergusia"; and the book is recommended by the reviewer particularly to readers with a burning interest in certain aspects of the work of Burrows, Carrel, Crile, et alia. Reginald the office boy has murmured that Velikovsky might be mentioned.

JANE OPPENHEIMER

LABORATORY DIRECTIONS FOR GENERAL BIOLOGY. *By Laurence C. Woodruff and Ruth E. McNair. Wm. C. Brown Co., Dubuque, Ia.* $1.35 (paper). iv + 69 pp.; ill. 1947.

This manual contains 15 exercises for a one-semester college course, planned to require a minimum of individual effort from the student. In most cases drawings are provided to be labeled; rarely does the student himself have to make a drawing, and then only of the simplest things. Most of the experiments are performed as demonstrations, the students recording the results and answering a few questions. The Survey of the Living World is given in one exercise that includes both the plant and animal kingdoms in their entirety. The exercise on Genetics consists solely of counting ratios (3:1 and 9:3:3:1) and working a few problems. I have seen Biology Laboratory Manuals and Workbooks for high school courses immeasurably superior to this. It would be uncharitable to mention where the course is taught.

BENTLEY GLASS

FUNDAMENTAL ACTIVITIES IN BIOLOGY. *A Workbook and Laboratory Manual for Use With Any Textbook. By Edwin L. Harer and Chelsey G. Remley. Republic Book Co., New York.* 96 cents (paper). x + 302 pp.; ill. 1947.

This workbook and laboratory manual is keyed to be used with any of the widely used high school biology textbooks. It is extraordinarily complete in coverage. Perhaps the major criticism which could be made of it is that the workbook aspect rather completely dominates the laboratory manual. The Appendix contains, among other features, a section on Audio-Visual Aids and another on Special References and Pamphlets that will be of considerable service to the teacher.

BENTLEY GLASS

BIOLOGY: HISTORY AND BIOGRAPHY

DIE ENTWICKLUNG DER MAKROSKOPISCH-ANATOMISCHEN PRÄPARIERKUNST VON GALEN BIS ZUR NEUZEIT. *By A. Faller. S. Karger, Basel.* S. fr. 15.-(paper). iv + 115 pp.; ill. 1948.

This excellent monograph describes the instruments used in gross anatomy from antiquity to the present. It narrates the evolution of the techniques of maceration, injection, corrosion, transparency, and macroscopical dyeing. The author does not claim completeness of data, but he comes rather close to it for the 17th century. He has paid relatively little attention to Galen's wealth of techniques. Otherwise he would not give credit to Spieghel for the first corrosion work on the liver. The subject-matter is fascinating to anyone who has ever had any contact with gross anatomical technique (and most biologists have), and the author, who is professor of histology at Fribourg, Switzerland, has handled his subject well. The illustrations are an integral, and not the least valuable part of the book, which is completed by a good chronological table, an index, and a bibliography.

ERWIN H. ACKERKNECHT

EVOLUTION

INTROGRESSIVE HYBRIDIZATION. *By Edgar Anderson. John Wiley & Sons, New York; Chapman & Hall, London.* $3.00. x + 109 pp.; ill. 1949.

In the author's words, the object of this book is an "attempt to take the whole problem (of hybridization in evolution) outside the area of argument and opinion and into the zone of measurement and analysis." Partly because of the controversial nature of some of the interpretations which are suggested but more particularly because a fruitful method of attack upon the problem is outlined, the author's conclusions should be stimulating to geneticist, taxonomist, and plant breeder alike. The book is likely to encourage a new interest in the collection of detailed and critical information.

The arguments presented may be summarized briefly as follows: In a hypothetical system of completely independent genes the number of different recombinations resulting from segregation reaches astronomical figures. In actual systems, as a consequence of linkage, the number of recombinations is greatly reduced, and though still large, is probably smaller than has been commonly realized. When differences between characters of two species are determined by many genes, the parental characters will tend to cohere in the generations which result from backcrossing or selfing their hybrid. If the parental species differ considerably in

ecological requirements, only a small fraction of the already greatly restricted recombinations will be adapted to the available ecological niches. The successful types will be usually those recombinations which resemble rather closely the parental species. Exceptions to this rule are to be found where man has "hybridized the habitat" (e.g., by cultivation), thus producing new artificial combinations of physiological conditions not normally provided in nature. Under such conditions hybrid combinations have a greater chance of survival. Since for the most part the frequency of established hybrids will be low relative to the frequencies of the parental species, subsequent generations will consist of a series of recurrent backcrosses of the hybrids to one or other of the parents. The net effect will be a restricted transfer of various gene combinations from one species to the other—a process termed by the author "introgression." This will manifest itself as an increased variability of the recurrent parent species. Moreover, the variation will be unidirectional and not at random, i.e., it will consist of a complex of associated deviations, held together by linkage, and having the characteristics in a modified degree of the donor parent species from which it was derived. It should be possible, therefore, to develop objective techniques of measurement to assess the amount of introgression which has taken place. In favorable material it may even be possible to deduce the probable characters of the unknown donor species from a careful study of such deviations in the recurrent species.

After reading the book, one is left with at least a suspicion that the barrier between species may not be as "near-absolute" as is commonly considered to be the case, but one is not convinced that linkage per se is the basic mechanism for reducing recombination between them. Certain theoretical examples presented as a demonstration of the importance of linkage do not appear to be valid, or, at least, the data can be interpreted differently.

In spite of such controversial issues or perhaps because of them, the book holds the reader's interest from cover to cover. The ingenious techniques of measurement developed from a basically simple scatter diagram excite admiration and offer a widely adaptable method of recording otherwise subjective taxonomic observations in an objective and precise manner with a view to interpreting them genetically. It suggests a method of attacking problems of speciation in which the possibilities of cytological and genetic analysis are seriously limited by the material, and in which conventional taxonomic analyses are necessarily empirical.

S. G. STEPHENS

GENETICS AND CYTOLOGY

INTRODUZIONE ALLO STUDIO DELLA GENETICA PER MEDICI, AGRARI E NATURALISTI.

By Carlo Jucci. Ulrico Hoepli, Milan. L.900.—(paper). xxiv + 420 pp. + 11 plates; text ill. 1944.

The author's opening remark is that a more correct title for this book could be "An Introduction to General Biology from the Standpoint of Genetics." It is, in fact, a book in which a wealth of factual information is marshalled so originally to illustrate general principles that it makes most delightful and interesting reading. Perhaps it may not be an advisable textbook for students, but it is certainly an excellent one for teachers. Among its many valuable features, I mention the following few:

Biochemical genetics is dealt with in one chapter, summarizing as an example the author's own work in the genetics of carotenoid and flavone pigments in the silkworm. There is not one relevant aspect of present biochemical genetics which cannot be illustrated clearly by this work. In particular, it brings out the importance of the genetic control of permeabilities, which is so conspicuously forgotten in most of the recent developments in this field. Gene control of morphogenesis is dealt with extensively (120 pp.) in both plants and animals: these six chapters are perhaps the best available review of this subject. About one-third of the book deals with the genetics of parasitic and symbiotic relationships, and here again the broad and happy choice of examples makes it a most valuable summary.

This book will be a very useful reference for teachers of genetics who wish to keep certain relations of genetics to general biology in the right perspective.

G. PONTECORVO

GENERAL AND SYSTEMATIC BOTANY

JOURNAL OF EXPERIMENTAL BOTANY. *An Official Organ of the Society for Experimental Biology. Volume I, Number 1.*

Edited by T. A. Bennet-Clark. Editorial Committee: E. Ashby, G. E. Blackman, R. Brown, F. G. Gregory, W. O. James, W. H. Pearsall, R. D. Preston, and M. Thomas. Published by Geoffrey Cumberlege, Oxford University Press, London. Subscription price 35s. per volume. Single numbers 14s. net. Three numbers per volume annually. No. 1: 131 pp. + 5 plates; text ill. March 1950.

According to the editorial policy, this new journal is "a medium for the publication of papers in the field of plant physiology, biochemistry, biophysics, experimental agronomy and related topics." The format and style are those characteristic of the Clarendon Press. The contents of the first issue are as follows:

two articles by Gregory, Milthorpe, Pearse, and Spencer on Experimental Studies of the Factors Controlling Transpiration; two Studies in Stomatal Behavior, one by Heath, and the other by Williams; The Path of Carbon in Photosynthesis, by Benson and Calvin; Demonstration of Compound Cilia in a Fern Spermatozoid by Means of the Ultra-violet Microscope, by Manton; Acid Metabolism of *Aspergillus niger*, by Allsopp; and The Effects of Sugar and Potassium on Extension Growth in the Root, by Brown and Sutcliffe.

GENERAL AND SYSTEMATIC ZOOLOGY

PROCEDURE IN TAXONOMY. *Including a reprint in translation of the Règles Internationales de la Nomenclature Zoölogique (International Code of Zoölogical Nomenclature) with titles of and notes on the Opinions rendered to the present date (1907 to 1947). Completely indexed. Revised Edition.*

By Edward T. Schenk and John H. McMasters; revised edition enlarged and in part rewritten by A. Myra Keen and Siemon William Muller. Stanford University Press, Stanford, Cal.; Geoffrey Cumberlege, Oxford University Press, London. $2.50. viii + 93 pp. 1948.

This small work comprises directions for the preparation of manuscript for papers on systematic zoology; an introduction to the rules of nomenclature, and a republication of the rules. Being concerned primarily with details of manuscript form and of nomenclature, its title appears to be seriously misleading. That nomenclature is a part of taxonomy is clearly stated (p. 2), but taxonomy is then said to be equivalent to systematics. Except for its footnotes, which list some distinguished examples of systematic works, the book is thereafter limited to a discussion of editorial procedure and to nomenclature rather than to the principles of classification, which seem to the reviewer essential to a discussion of "Procedure in Taxonomy." It is perhaps not invidious to point out that the title of a work on editorial practice should be short, and that subtitles in scientific works (which require the writing of bibliographic references) should be composed so as not to require punctuation, or else should be punctuated. The trivia of nomenclature and of form of manuscript are discussed without humor or insight. It is one of the curses of taxonomy that complete nonsense, placed in correct form, may become part of its literature.

By means of the instructions in this book a young zoologist might draw up the description of a new species of animal for publication, or might present the reclassification of an old one in acceptable form. The systematic categories, the nomenclature of types, the storage of type specimens, the distinction between specific and trivial names, and Latin terms and abbreviations are discussed in 31 pages. There are 37 pages for the International Rules of Zoological Nomenclature, and 22 pages of index.

Even in a work whose scope is so specifically limited, it should have been pointed out that the taxonomic procedures described are the rules for playing a game. The game is, indeed, a distinguished one, engaged in by a world-wide group of players, and the rules are elaborate, international, and often obscure. Inadequate and premature descriptions of new species, prepared precisely according to the rules, or resurrections of long defunct names (also according to rule) rushed to the press in order to "win," do not constitute a contribution to systematics but are part of a game.

Descriptive zoology and botany are under fire in university circles throughout the world, perhaps mainly because we systematists have ourselves failed to distinguish the game from science, or bad work from good. There seems at last to be a revolt of major proportions against certain hitherto accepted operations under the nomenclatural rules, with which some members of the International Commission itself are in sympathy. What is at issue is the establishment of an Official List of generic and trivial names not subject to change, in a renewed effort to achieve a stabilization of nomenclature. That such stabilization has not been achieved, even for common species, during nearly 50 years of operation of the International Rules, is a major disgrace to systematic zoology, and reflects the fact that naming and name-changing have been so fascinating a game that even very eminent zoologists have pursued it to the detriment of zoology.

KARL P. SCHMIDT

ANIMAL MORPHOLOGY

THE ABC'S OF ANATOMY: *The anatomy of the human body simplified.*

By Elmer J. Tomasch. William-Frederick Press, New York. $3.50. iv + 24 pp. + 100 plates. 1947.

This little book is an attempt to present the human body anatomically to the artist. Semi-schematic drawings of the skeleton, in whole and in part, comprise the first portion of the book. Those muscles important to an appreciation of surface anatomy are shown in the next part, in textbook fashion and schematically arranged on the skeleton. The last portion stresses the main masses and rhythms of the human body. The anatomy is in large part adequately illustrated, and it is presented in a helpful and ingenious manner. It is unfortunate that the author has completely ignored the female, and that as an ideal body, he has chosen the unesthetic exaggerations of the weight-

lifting "muscle man." The book also suffers from being over-priced.

JAMES M. SPRAGUE

CONCISE ANATOMY.

By Linden F. Edwards. Blakiston Co., Philadelphia and Toronto. $5.00. xxiv + 548 pp. + 2 plates; text ill. 1947.

This is another textbook to add to the many which attempt to present the anatomy of the human body for the use of students in physical therapy, occupational therapy, medical technology, nursing, dental hygiene, physical education, etc. The actual descriptive part of the book, which comprises about two-thirds of the text, is an accurate, "boiled-down" version of a standard medical textbook of gross anatomy. Almost all of the many illustrations have been taken from standard textbooks. The first one-third of the book consists of a general introduction to embryology, histology, and neurology. The material is well organized, and the data are frequently grouped in tables helpful to the beginning reader. Throughout there is an appreciation of function. The bibliography consists almost entirely of textbooks, but they are well chosen. Even so, the omission of citations of the research literature removes the atmosphere of movement and of change in this part of the world of science, and the result is a static picture.

JAMES M. SPRAGUE

SYNOPSIS OF GENERAL ANATOMY.

By Linden F. Edwards. Blakiston Co., Philadelphia and Toronto. $2.75 (paper). xvi + 151 pp. + 1 plate; text ill. 1948.

The ultimate stage in "boiling down." This ought to be very helpful to any student eager to absorb the minimum knowledge of the subject necessary to pass the final examination, or to one who cannot otherwise see the forest because there are too many trees. The *Synopsis* is well organized and competently prepared.

ILLUSTRATIONS OF REGIONAL ANATOMY. *I. Central Nervous System. II. Head and Neck. III. Abdomen. IV. Pelvis. V. Thorax. VI. Upper Limb. VII. Lower Limb. Seventh Edition.*

By E. B. Jamieson. Williams & Wilkins Co., Baltimore. Complete set, $20.00 (paper); (I) $3.50; (II) $4.00; (III) $3.00; (IV) $2.50; (V) $2.50; (VI) $3.00; (VII) $3.50. (I) iv + 51 plates + 2 pp.; (II) iv + 64 plates + 4 pp.; (III) iv + 44 plates + 2 pp.; (IV) iv + 35 plates + 2 pp.; (V) iv + 32 plates + 2 pp.; (VI) iv + 42 plates + 2 pp.; (VII) iv + 52 plates + 2 pp. 1947.

This loose-leaf atlas consists of 7 parts, comprising 51 plates of the central nervous system, 54 of the head and neck, 44 of the abdomen, 35 of the pelvis, 32 of the thorax, 42 of the upper limb, and 52 of the lower limb. The first edition, which appeared in 1934, consisted of the first five sections and 297 plates. The present edition is similar to the sixth, and has 320 plates, almost all of which are in color. Anatomical terms labeling the figures are in English. The figures, although not uniformly successful, are generally satisfactory, and are designed with an extensive use of sharp colors, to facilitate a rapid visualization of relationships and parts. The convenience of having the 7 parts bound separately and in loose-leaf form is considerable.

JAMES M. SPRAGUE

THE HEAD, NECK, AND TRUNK. *Muscles and Motor Points.*

By Daniel P. Quiring. Lea & Febiger, Philadelphia. $2.75. 115 pp. + 1 plate; text ill. 1947.

The present book is a companion volume to *The Extremities* by the same author, and is presented in similar manner. There is no text as such, but a brief description of the origin, insertion, function, innervation, and blood supply of the muscles accompanies each schematic drawing. The drawings are simple but clear, and the muscles are shown relative to the pertinent skeletal structures. The author gives the appropriate page references in Gray's and Cunningham's anatomies, where the student may find the original, detailed descriptions and more complete illustrations.

JAMES M. SPRAGUE

APPLIED ANATOMY OF THE HEAD AND NECK *For Students and Practitioners of Dentistry. Second Edition.*

By Harry H. Shapiro. J. B. Lippincott Co., Philadelphia, London and Montreal. $10.00. xvi + 303 pp.; ill. 1947.

The second edition of this very useful textbook has been extensively revised, as may be seen by comparing it with the first (cf. *Q.R.B.*, 19: 62, 1944), which had 189 pages and 173 figures, none in color. The new edition has 14 chapters (compared to 9 in the first); and there is a new presentation of the (1) teeth and dental arches, (2) nose and paranasal sinuses, (3) roentgenograms and anatomical landmarks, (4) glands of the head and neck, and (5) anatomy of oral infections. The chapter on development has been enlarged. The author shows an extensive knowledge of the research

literature, listing 389 references in the bibliography. Although this excellent work is designed primarily for the use of students of dentistry, the student of medicine will find it a most useful correlative reference book.

JAMES M. SPRAGUE

SURFACE AND RADIOLOGICAL ANATOMY *for Students and General Practitioners. Second Edition Rewritten.* *By A. B. Appleton, W. J. Hamilton, and Ivan C. C. Tchaperoff. Williams & Wilkins Co., Baltimore.* $7.00. viii + 332 pp.; ill. 1946.

This is an extensively rewritten second edition of the volume which appeared earlier (cf. *Q.R.B.*, 14: 95, 1939) under the authorship of Appleton, Hamilton, and Tchaperoff. The present work is extensively illustrated by 390 figures (51 in color), of which 190 are radiographs. There is an introductory chapter on general anatomy and methods, and separate and detailed consideration is given to the upper limb, the chest and back, the abdomen, the head and neck, the vertebral column, and the lower limb. This scholarly work can scarcely be commended too highly as a background of physical diagnosis for both student and practitioner.

JAMES M. SPRAGUE

ANIMAL PHYSIOLOGY

LE SANG. *"Que Sais-je?" Le Point des Connaissances Actuelles.* *By Louis Van Den Berghe. Presses Universitaires de France, Paris.* 30 fr. (paper). 128 pp.; ill. 1946.

This small, well-printed book on blood is published in a series intended for the general public rather than for specialists, physicians, or medical students. It is written clearly and simply and manages to convey much useful information in spite of its small size. There is a brief historical introduction followed by a chapter on the functions of blood, with a simple exposition of the transport of oxygen and carbon dioxide. The normal constituents of blood—both cellular and chemical—are then discussed. Next there is a chapter on the origin and development of the cellular elements, followed by one on their functions and fate. A few pages are given to comments on the pathological variations of these cellular elements. The blood groups and transfusions are more extensively presented, and brief mention is made of the Rh factor. The concluding chapter gives some insight into current methods of investigation available for problems relating to blood. The text is well illustrated with diagrams and drawings, and there are a few tables. Historical aspects are not overlooked. The author has made good use of comparative physiology in emphasizing certain points.

F. CHINARD

BLOOD CLOTTING AND ALLIED PROBLEMS. *Transactions of The Second Conference, January 24-25, 1949, New York.* *Edited by Joseph E. Flynn. Josiah Macy, Jr. Foundation, New York.* $2.25 (paper). 231 pp.; ill. 1949.

This conference was attended by 19 participants, all actively investigating problems concerned with blood coagulation, and representing such varied fields of medicine as anatomy, pathology, physiology, and biochemistry, as well as clinical medicine. The report includes the text of 8 formal papers, as well as a full transcript of the discussions, which were extensive and informal. The papers of major importance included reports of a thromboplastin-inhibitor (Tocantins and Carrol; Overmann); the formation and structure of the fibrin-clot (Ferry); the effects of the surface (of containers) on blood coagulation (Barker and Margulies); factors which influence the rate of conversion of prothrombin to thrombin (Flynn and Standley); and current views regarding the function of the blood platelets (Quick). There is also an extensive discussion of methods of standardizing thromboplastin preparations, with special reference to determination of the prothrombin time.

Great advances have been made in our knowledge of blood coagulation during the past decade, but a great deal more remains to be done before a clear comprehension of the process can be attained. Many different substances are concerned, enzymes and proenzymes, initiators, accelerators, and inhibitors, and few of these have been adequately characterized chemically or even obtained in a relatively pure state. The nomenclature is confusing, since different names have been applied by various investigators to what are presumably identical substances. The experimental technic is tricky and difficult at best, since there are variable factors which are not adequately understood and are difficult to control, and apparently slight differences in the set-up of the experiments may yield divergent results in different laboratories. Under such circumstances it is inevitable that there should be sharp differences in interpretation, and these are brought out in the discussions freely and frankly, and sometimes vehemently.

The Transactions contain no concise or systematic discussion of the subject as a whole, and readers who do not have a fair preliminary knowledge will find the going heavy and perplexing. Those who are better oriented will find this a valuable source of information regarding the status of the subjects discussed, as at

the date of the Conference. For such it is highly recommended.

PAUL W. CLOUGH

BLOOD CLOTTING AND ALLIED PROBLEMS. *Transactions of The First Conference, February 16–17, 1948, New York.*

Edited by Joseph E. Flynn. Josiah Macy, Jr. Foundation, New York. $3.25 (paper). 179 pp.; ill. 1948.

This conference served as a model of the Second Conference, the Transactions of which are discussed above. The Transactions are opened by an excellent summary (by Jaques) of those facts concerning hemostasis and coagulation which are definitely or reasonably well established. He has not attempted a critical analysis of the present status of the more newly discovered factors which are under active investigation and concerning which there is much controversy—some of it acrimonious.

The formal papers include reports regarding fibrinolytic enzymes (Astrup); factors initiating and accelerating thrombosis (Brinkhous); "unsolved problems," concerned chiefly with the chemistry and physical make-up of the fibrin clot (Edsall); protein equilibrium reactions in the blood clotting mechanism (Seegars and Ware); and the value of prothrombin determinations (Wright, Bramble, Olwin, Quick, Smith, Luck, individually). A highly useful feature is the inclusion, in the appendix of the precise technic used in determining prothrombin in 8 different laboratories.

Although this work is now over 2 years old, those interested in this field will find it still a valuable source of pertinent information not easily accessible elsewhere.

PAUL W. CLOUGH

STUDIES ON DIETARY AND OTHER FACTORS AFFECTING THE SERUM-CALCIUM LEVELS OF SHEEP. *Bull. No. 240, Parts I to VI, Coun. sci. ind. Res., Commonw. Austral.*

By M. C. Franklin, R. L. Reid, and I. L. Johnstone. Council for Scientific and Industrial Research, East Melbourne, Australia. Free upon request (paper). 77 pp. 1948.

ANIMAL NUTRITION

ADVANCES IN FOOD RESEARCH. *Volume I.*

Edited by E. M. Mrak and George F. Stewart. Academic Press, New York. $7.50. xvi + 459 pp.; ill. 1948.

In this volume twelve contributors have discussed the following subjects: the physiology and chemistry of rigor mortis, with special reference to the aging of beef; factors influencing the vitamin content of canned foods; the physiological basis of voluntary food intake (appetite); biochemical factors influencing the shelf life of dried whole eggs and means for their control; factors affecting the palatability of poultry, with emphasis on histological post-mortem changes; the deterioration of processed potatoes; the influence of climate and fertilizer practices upon the vitamin and mineral content of vegetables; non-enzymatic browning in fruit products; microbial inhibition by food preservatives; and high-polymer pectins and their de-esterification.

Investigators in food research have quickly applied to the problems of food technology all of the new discoveries in biochemistry and other biological sciences. Their publications are dispersed, and are often not available to those who could profit by reading them. The annual volume, in which experts prepare review articles, has become a necessity in a number of fields of science and technology. The present volume sets a high standard, and its usefulness is assured.

E. V. MCCOLLUM

BIOCHEMISTRY

ADVANCES IN PROTEIN CHEMISTRY. *Volume V.*

Edited by M. L. Anson and John T. Edsall. Associate Editor for the British Isles: Kenneth Bailey. Academic Press, New York. $7.50. ix + 481 pp. 1949.

The present volume of this valuable series begins with a discussion of methods of peptide synthesis in vitro, by Joseph S. Fruton, in 75 pages which include extensive tables of the optical rotation and melting points of known peptides. There follows a critical survey of methods of amino acid analysis of proteins, by G. R. Tristram. The formidable difficulties of this subject are attested by a vast literature. "Progress was delayed for many years because methods of analysis were, in the main, based upon the gravimetric principles of elementary analysis, and analysts only slowly realized the difficulties which attend the quantitative isolation of a single constituent or any of its derivatives from biological materials. In recent years the development of new methods, micro in scale, based upon many novel principles (e.g., isotope dilution, microbiological assay, partition chromatography) has revolutionized amino acid analysis," so that it is now reasonable to hope "that valuable information will be obtained upon the amino acid stoichiometry of proteins." However, the new methods are to some extent still in the developmental stage and are by no means without their special difficulties. Not the least of the difficulties

still remaining are the means of establishing evidence of significant purity of the protein to be analyzed, and of avoiding loss or alteration of the residues during hydrolysis. However, "while there are still differences in the results of analysis the degree of agreement is remarkable and, for the first time in the history of amino acid analysis, it is possible to make use of amino acid data with justifiable confidence." Tristram then develops an interesting but necessarily highly tentative discussion of initial inferences regarding protein structure from the evidence of amino acid analysis. Much weight is given to the concept of separate peptide chains, from the evidence for terminal groups derived from the work of Sanger and others. If there are separate polypeptide chains, other evidence seems to require that they be united by covalent linkages, which might be disulfide bonds, but do not seem to be so in some cases at least. "... The stoichiometry of proteins follows no simple rule (such, for instance, as that propounded by Bergmann and Niemann)."

The biological evaluation of protein is discussed by J. B. Allison, in a review of nitrogen balance studies and protein effects upon growth and tissue regeneration. One of the most interesting points emerging from this rapidly growing field has been put as follows: "If it is true that essential amino acids are not stored individually in the tissues ..., and if, moreover, the synthesizing mechanisms which fabricate complete tissue proteins must have available all the necessary building stones..., it would seem likely that the synthesizing mechanisms operate on a 'perfectionist' or 'all or none' principle to the extent that if they cannot build a complete protein when one is required they will build none at all. This would suggest also, that the process of synthesis must be total rather than partial, and to be effective the synthesizing mechanism must have available and practically simultaneously all the essential amino acids in adequate proportions and amounts.

There is a relatively short descriptive survey of milk proteins by T. L. McMeekin and B. D. Polis, followed by a broad discussion of plant proteins and protein metabolism in plants, by J. W. H. Lugg. Among the points brought out here is the fact that, with certain exceptions, the bulk proteins of plants appear to be of somewhat similar amino acid composition, in contrast to the bulk proteins of seeds which are of distinctly dissimilar composition. Plant proteins, like animal proteins, are being continually broken down and rebuilt. The important question, whether synthesis is the reverse of catabolism, or whether the processes constitute a cycle involving different routes, can perhaps be approached advantageously in plants.

There are articles on synthetic fibres made from proteins, by Harold P. Lundgren, and protein chemical aspects of tanning, by K. H. Gustavson. Finally, lest we become complacent, Albert Claude contributes a brief consideration of proteins, lipids, and nucleic acids in cell structures and functions. He says: "The most significant development in recent years has been the demonstration that important cell functions are segregated in mitochondria and homologous large granules." It has been shown that the cytochrome system which utilizes molecular oxygen is localized in these elements, probably exclusively. Also D-amino acid oxidase, the fatty acid oxidase system, and members of the Krebs cycle have been shown to be segregated in mitochondria. It seems possible that the energy derived from anaerobic glycolysis, on the other hand, is mediated through ribonucleic-acid-containing elements in the cytoplasm.

EVELYN HOWARD

LES LIPIDES. *Paris, 5 au 12 Janvier 1948, XI. Colloques Internationaux du Centre National de la Recherche Scientifique.*

Centre National de la Recherche Scientifique, Paris. 1000 fr. (paper). 399 pp. + 3 plates; text ill. 1949.

This volume presents the proceedings of an international colloquium on lipids held in Paris in January 1948. The contents have already been published as the first four numbers of volume II of the *Archives des Sciences Physiologiques* (1948). The volume is divided into eight sections, each of which contains one or more general reviews followed by a more detailed presentation of recent experimental work. The section headings, which indicate the scope of the symposium, are: (1) digestion and intestinal absorption, (2) deposition and mobilization of reserve fats, (3) lipid transport in the blood; lipoprotein linkages in blood and tissues, (4) metabolism of the higher fatty acids, (5) desaturation of the higher fatty acids and of the essential fatty acids, (6) role of the lipids in blood coagulation, (7) phosphoaminolipids and their degradation products, and (8) the problem of the oxidation of fats and antioxidants.

Of the 26 communications by 24 scientists, 19 are in French and 7 in English. Though it is not possible to describe all of them, a few may be mentioned as particularly interesting. Macheboeuf has contributed an extensive review of his work on the lipoproteins of blood, this being followed by a review on cellular lipoproteins by Chargaff. Frazer, who elsewhere in this volume discusses his work on the digestion and absorption of fats, presents his work on artificial lipoproteins and reports some new observations on hemoglobin-detergent complexes. Barnes and Gurin review the formation and utilization of ketone bodies. Barnes also contributes one of the three papers on antioxidants. Though the material presented does not cover every facet of the field of lipids, this book should interest workers in lipid chemistry and lipid physiology.

F. CHINARD

PARTITION CHROMATOGRAPHY. *A Symposium Held at London School of Hygiene and Tropical Medicine on 30 October 1948. Biochemical Society Symposia No. 3. Organized and edited by R. T. Williams, assisted by R. L. M. Synge. Cambridge University Press, London and New York.* $1.50 (paper). 103 pp. + 1 plate; text ill. 1950.

The introduction is followed by eight chapters, as follows: Some Theoretical Aspects of Partition Chromatography, by A. J. Martin; Application of Partition Chromatography to the Study of Protein Structure, by F. Sanger; Partition Chromatography and its Application to Carbohydrate Studies, by S. M. Partridge; Anthocyanins, Flavones and other Phenolic Compounds, by E. C. Bate-Smith; Partition Chromatography of Organic Acids, Purines and Pyrimidines, by R. S. Elsden; Partition Chromatography with Stationary Phase Other than Pure Water, by A. A. Levi; General Review of the Applicability of the Method, by R. L. M. Synge. There is a supplementary bibliography, which extends citations beyond the references given at the end of each chapter. This covers Review Articles; Technique; Amino-Acids, Peptides, Proteins and their Derivatives; Carbohydrates and Related Substances; and Other Substances. This series of articles by distinguished investigators in the field of this mightiest of all analytical tools of the chemist is a highly valuable contribution.

E. V. MCCOLLUM

FATTY ACIDS ANTIBACTERIALS FROM PLANTS. *Carnegie Institution of Washington Publication 586. By H. A. Spoehr, J. H. C. Smith, H. H. Strain, H. W. Milner, and G. J. Hardin. Carnegie Institution of Washington, Washington, D. C.* 75 cents (cloth); 50 cents (paper). iv + 67 pp.; ill. 1949.

MICROBIOLOGY

ANNUAL REVIEW OF MICROBIOLOGY. *Volume III. Edited by Charles E. Clifton, Sidney Raffel, and H. Albert Barker. Annual Reviews, Stanford, Cal.* $6.00. viii + 476 pp.; ill. 1949.

The third volume of this series is the best to date. Among the 18 reviews included, there is a remarkably high proportion of first-rate critical essays. Particularly noteworthy are: Bacterial Variation (J. Lederberg); The Morphology, Cytology, and Taxonomy of the Actinomycetes (D. Erikson); Ciliated Protozoa; Cytogenetics, Genetics and Evolution (T. M. Sonneborn); Types of Acquired Immunity against Infectious Disease (S. Raffel); and The Growth of Bacterial Cultures (J. Monod). Other topics discussed include: Metabolism of Microorganisms (W. W. Umbreit); Nutrition of Microorganisms (E. E. Snell); Constituents of Viruses (C. A. Knight); Action of Antibiotics *in vivo* (W. C. Cutting); The Cellular Basis of Immunity (W. H. Taliaferro); Virulence and Pathogenicity (D. W. Watson and C. A. Brandly); Chemistry of Toxins (L. Pillener and K. C. Robbins); Nature and Variability of Disease Resistance in Plants (H. Hart); Oral Microbiology (R. W. Harrison); Dermatotropic Viruses (G. J. Buddingh); Food Microbiology (H. O. Halvorson); Recent Development in Microbiological Techniques (L. S. McClung); and Bacteriophage (J. Fong).

R. Y. STANIER

INVENTAIRE ET DESCRIPTION DES BACILLES PARATUBERCULEUX. *By Paul Hauduroy. Masson et Cie., Paris.* 400 fr. (paper). iv + 168 pp. 1946.

Some 160 species and strains of Mycobacteria are herein described, the descriptions being given in alphabetical order of the names of the individuals who first reported them. Many very imperfectly characterized isolates are included. *Mycobacterium tuberculosis, M. paratuberculosis* (Johne's bacillus), and the various acid-fast organisms isolated from the lesions of leprosy have been excluded from the descriptions. Although many of the paratubercular organisms were isolated from human or animal pathological material, only a minority are pathogenic to laboratory animals. Other characteristics are discussed, particularly the source from which the bacilli were isolated (habitat). There is an interesting tabulation and discussion of cross reactions between various "paratuberculins" and true tuberculins in animals and in man.

The book should be of great value to specialists in the taxonomy and identification of Mycobacteria. It will be of considerable collateral interest to those working in the field of experimental tubercular infections.

WALTER C. TOBIE

HEALTH AND DISEASE

RICKETTSIAL DISEASES OF MAN. *A Symposium on the Rickettsial Diseases of Man, Organized by the Section on Medical Sciences of the A. A. A. S. and Presented at the Boston Meeting on December 26–28, 1946. Organized by Malcolm H. Soule; edited by Forest Ray Moulton. American Association for the Advancement of Science, Washington, D. C.* $6.25 ($5.25 to AAAS members). iv + 247 pp.; ill. 1948.

This volume consists of 27 papers prepared by as many authors for a symposium organized by the Section on Medical Sciences of the AAAS and presented at the Boston Meeting on December 26–28, 1946. The series of papers, each concerned with a different phase of the

subject, constitutes a comprehensive and thorough review of the rickettsial diseases. The authors are recognized authorities, many of them being investigators who have spent years studying the subjects upon which they write.

Investigators during World War II contributed greatly to our knowledge in regard both to the nature of rickettsiae and the methods of control of the infections. Those advances are particularly stressed in the present volume. The discussions range from certain basic aspects of the study of rickettsiae, such as are contained in the papers on their general biologic character and their classification, through descriptions of the clinical aspects of the various diseases, their pathology, treatment, epidemiology, arthropod vectors, and reservoirs of infection. Also included are descriptions of the various methods of laboratory diagnosis, preparation of vaccines, and control of vectors.

Most of the papers are well illustrated with maps, graphs, patient's charts, or tabulated matter as is appropriate. References are given at the end of each paper. As with many volumes of this kind, i.e., those composed of chapters by a number of contributors, no index is included. Although perhaps understandable, the omission is regrettable, because the book will find its greatest value as an authoritative reference work. Nevertheless, it serves admirably to mark the progress of knowledge in the field of rickettsial diseases, and will long remain a highly valuable source of information.

FRANCIS B. GORDON

COCCIDIOSIS. *Ann. N. Y. Acad. Sci., Volume 52, Article 4.*

Edited by Sterling Brackett; by 44 authors. The New York Academy of Sciences, New York. $3.00 (paper). Pp. 429–624 + 1 plate; text ill. 1949.

This publication consists of papers presented at a conference held at the New York Academy of Sciences, March 4–5, 1949, under the chairmanship of Sterling Brackett. Limitations of space prevent a complete description of all the 28 pages. A critical evaluation of the quality of the contributions may be left to specialists. Nevertheless, the publication is an important one on account of the tremendous economic losses caused by coccidial infections in livestock. The compilation will probably exert a useful influence for many years to come.

WALTER C. TOBIE

LA MÉDECINE INFANTILE. *Collection Armand Colin (Section de Biologie), Number 234.*

By Robert Broca. Librairie Armand Colin, Paris. 100 fr. (paper). 188 pp.; ill. 1943.

This pocket-size volume covers infectious diseases, endocrinology, nutrition, and congenital diseases from a pediatric point of view. One chapter is devoted to acrodynia. As of the time of publication, it seems well up to date. Authors and dates are mentioned freely in the text, but references are lacking except for a list of 40 books. Those interested in French clinical views may find the book of some incidental significance. To the average American biologist (if indeed there is such an individual) it offers little of value.

WALTER C. TOBIE

PSYCHOLOGY AND ANIMAL BEHAVIOR

INTRODUCTION TO METHODS IN EXPERIMENTAL PSYCHOLOGY. *The Century Psychology Series. Second Edition.*

By Miles A. Tinker. D. Appleton-Century Co., New York and London. $4.00 (paper). viii +232 pp. + 2 plates; text ill. 1947.

"About 30 per cent of the material in the revision is new or different from that in the original edition. The major changes are as follows: chapters on the Estimation of Temporal Intervals, Self-Rating of Personal Traits, and The Adjustment Inventory has been dropped. New chapters on Clerical Aptitude, Social Attitudes, and Measurement of Introversion-Extroversion have been added. There has been thorough revision of sections on variability, art aptitude, and, in part, correlation. . . ."

PSYCHOLOGICAL WARFARE.

By Paul M. A. Linebarger. Infantry Journal Press, Washington, D. C. $3.50. xvi + 259 pp.; ill. 1948.

The author has compiled what he modestly calls a "patchwork of enthusiastic recollection" of his experience of five years as "civilian expert and as an army officer in American psychological warfare facilities—at every level." His work is based on experience rather than research, on practice rather than on theory. He treats his subject in an informal, pithy, and newspaperish style. The result, however, is considerably more than a "patchwork," for sooner or later he discusses all critical phases of psychological warfare from the practical propagandist's point of view. Linebarger's survey is divided into three principal sections: Definition and History; Analysis, Intelligence, and Estimate of the Situation; and Planning and Operations. This book is practically the only available general source of information concerning the whole program of psychological warfare conducted during World War II, and for this reason it will be read by many who are

curious as to the successes and failures of psychological warfare as an adjunct to military operations. The publication of this book is a small but significant reaffirmation of the importance of ideas over weapons in ideological struggles, a salutary reminder in a period when political offense and defense in the competition of ideas have come, almost pathologically, to depend upon armed violence.

JOSEPH C. FRANKLIN

THE STORY OF HYPNOTISM.

By Robert W. Marks. Prentice-Hall, New York. $3.00. xii + 246 pp. 1947.

This is a popularized but very complete and accurate report on hypnosis, its recognition as a psychic phenomenon, and its development as a social phenomenon. The author first orients the reader on the subject by defining hypnosis, mostly through description of the induction stages. He then takes up Mesmer and the succession of physicians after him who used hypnosis in one form or another. He presents faith cures as a form of suggestion. Without being dogmatic or belligerent, he ascribes spiritualism, religious mysticism, and ecstasy to forms of hypnosis. The final chapter is devoted to hypnosis as a factor, through mass suggestion, in our present social structure—Goebbel's propaganda, for example, acting as an hypnotic influence on the minds of the German people. Marks has made no attempt to sensationalize his subject, although it is a topic which lends itself to such exploitation. His restraint and good taste are commendable.

HELEN ARTHUR

PROBLEMS OF EARLY INFANCY. *Transactions of the Second Conference, March 1–2, 1948, New York. With Supplement Covering Special Meeting, July 18–19, 1947, New York.*

Edited by Milton J. E. Senn. Josiah Macy, Jr. Foundation, New York. $1.00 (paper). 120 pp.; ill. [No date.]

PROBLEMS OF INFANCY AND CHILDHOOD. *Transactions of The Third Conference, March 7–8, 1949, New York.*

Edited by Milton J. E. Senn. Josiah Macy, Jr. Foundation, New York. $1.25. 156 pp. 1949.

These publications are reports of two conferences sponsored by the Josiah Macy, Jr. Foundation. The conferences are part of the Foundation's program for furthering scientific knowledge by having workers in different areas of a given field meet to exchange ideas and points of view. In this instance the topic of infancy and early childhood involved the efforts of 25 well-known pediatricians, psychiatrists, obstetricians, and psychologists. These people met for two days in 1948 and 1949, and the papers presented, with the attendant discussion, are faithfully reproduced here. The effect is almost like being actually present in the serious but informal business of working through to some general understanding of concepts that affect these several disciplines.

In 1948 the main concern was the effect on the infant of factors in pregnancy. Helen Deutsch discussed psychological problems of pregnancy. John Parks, Howard Walser, and Albert Vollmer reported from the obstetrician's point of view on the emotional factors in pregnancy, and how the relaxation method of childbirth affects the mother and baby. A supplement, added to the 1948 Transactions, reports a special meeting held in July 1947. In this a number of foreign physicians gave reports on what had happened in their countries to children in wartime and how those experiences are affecting their mental health today. These are quite moving, if rather simple, statements from Holland, France, Sweden, and Switzerland.

In 1949 only two prepared papers were given: one by Sibylle Escalona on The Psychological Situation of Mother and Child upon Return from the Hospital; the other, by Lucie Jessner and Samuel Kaplan, an Observation on the Emotional Reactions of Children to Tonsillectomy and Adenoidectomy. Both are important and provocative issues and caused a great deal of discussion. It is to be hoped that such an exchange of ideas does have the desired effect of strengthening the unity and the understanding of all the medical personnel who deal with expectant mothers, infants, and young children.

HELEN ARTHUR

THE RESPONSIVENESS OF KINDERGARTEN CHILDREN TO THE BEHAVIOR OF THEIR FELLOWS. *Monographs of the Society for Research in Child Development. Volume XI, Serial Number 43, Number 2, 1946.*

By Esther Kite Harris. Society for Research in Child Development, National Research Council, Washington, D. C. $2.50 (paper). viii + 184 pp.; ill. 1948.

This is another psychological monograph turned out with typical, if monotonous, competence. It follows the standard form, so there are no surprises in the presentation or in the conclusions summed up so efficiently in the last pages.

Using a pictorial Guess Who technique on 24 kindergarten children, plus their teacher's evaluations and parents' reports, Mrs. Harris is able to state that social responsiveness is a personality factor which is not related to age, I.Q., or sex. Even in kindergarten children, there is a wide range of social responsiveness—some preferring a small group of congenial friends and others a larger social orbit. The children gave evidence that their judgments on each other were largely deter-

mined by their own social indoctrination, whence follows the inevitable hint that children should be "rightfully guided and directed" so that their inherent social responsiveness will be harnessed to the best interests.

HELEN ARTHUR

KINDER UND JUGENDLICHE ALS ZEUGEN. *Psychologische Praxis: Schriftenreihe für Erziehung und Jugendpflege, Number 3.*

By Ernst Probst. S. Karger, Basel and New York. S. fr. 3.80 (paper). 55 pp.; ill. 1945.

This booklet, like the 4 others whose reviews follow, is a part of the Swiss series, Psychological Practice. These publications have been written for teachers, for educators, and for psychological therapists in the fields of child guidance, adolescent counseling, etc. Their purpose is "to guide and interpret the factors and forces encountered in actual practice but not to give theoretical explanations."

The editor of the entire series is the author of this publication. Its theme is the question: are the testimonies of children and juveniles as trustworthy as those of adults, or are their observations and statements to be doubted, either generally or in special cases? The author's conclusions are based on 30 cases in which he, as a school psychologist in Basel, acted as court-advisor. The conclusions may be summarized as follows:

(1) The judge should not base his decision on testimonies of children under 4 years of age. Reasons: the egocentric attitude, the lack of self-criticism, and the insufficient development of language prevailing in this age group.

(2) Between the ages of four and seven the following factors are likely to influence trustworthiness negatively: heightened suggestibility, strong feelings of sympathy or antipathy, tendency to exaggerate and confabulate. The advice given is to have those children questioned as soon as possible by experts in child psychology.

(3) In the group from seven to the beginning of puberty (eleven to thirteen) adverse influences are: the need for self-assertion, the desire to play a role, the desire to arouse attention. Incidents actually observed are fused with expectations and rumors. Day dreams, lack of self-criticism, and a tendency to dramatize call for special scepticism whenever sexual accusations are involved.

(4) The period of puberty may add to these factors a particular sense of justice: to betray a secrecy shared with one's companions is considered the worst crime. Yet even a friend suspected by others of some delinquent act is immediately condemned: the child's own inner insecurity and need for self-protection lead to public separation from the friend in self-righteous indignation.

(5) Simple, direct observation cannot find signs that mark the unreliable witness. A psychologist needs the expert interpretation of tests to evaluate intellectual development, memory, and affective behavior. The author worked with the Binet test; with the exposition of pictures for a few minutes, followed by 12 correct and 12 false (suggestive) questions; or with a similar procedure in recounting a brief story read. These tests were given to control groups in the classroom. Finally, he made use of the Rorschach test.

(6) Three protocols are given in some detail to demonstrate how a tendency to pathological living may reveal itself in one or another of these tests. The author, however, emphasizes the possibility that such a tendency may not always manifest itself in such tests as he carried out. The more tests are used and the more varied they are, the greater will be the chance to develop methods by which the general reliability of a witness can be recognized and graded.

WALTER O. JAHRREISS

PSYCHOLOGIE DER BERUFSBERATUNG. *Psychologische Praxis: Schriftenreihe für Erziehung und Jugendpflege, Number 4.*

By Richard Meili. S. Karger, Basel and New York. S. fr. 4.35 (paper). 64 pp. 1948.

This publication grew out of its author's great experience as a vocational psychologist and counselor. It is well written and reveals mature judgment and sincere concern. "Nobody," the author writes, "can be more keenly aware of the forces of our economic and social conditions than the vocational counselor; he has to take them into account and adjust to them lest he give futile advice. Yet, his real task remains to aid and assist the individual against the all-powerful machinery of modern society." The author makes intensive use of psychological tests and defends them against undeserved criticism. The fault usually lies, he thinks, with those psychologists who have neither the necessary experience to give a test carefully nor to interpret it, and not with the tests or their methods. "The essential traits and aptitudes of an individual manifest themselves in the most different situations and will not escape the scrutiny of exact tests and observations."

WALTER O. JAHRREISS

ENTWURZELTE UND DISHARMONISCHE KINDER. *Psychologische Praxis: Schriftenreihe für Erziehung und Jugendpflege, Number 5.*

By Karl Heymann. S. Karger, Basel and New York. S. fr. 4.35 (paper). 56 pp. 1946.

The American reader will find in this pook a distinctly European flavor. The dynamics of the disharmonic, the neglected, the uprooted and asocial juvenile behavior seem unduly simplified; nor will statements like the following be easily accepted: "In an individual with a certain hereditary disposition to abnormal physical reactions . . . an illness may manifest itself and its conditions may lead directly to stealing, just as directly as a sore throat to coughing"; some formulations may sound too metaphysical, even "existential." It may be strange to hear that there are certain professions for which the absence of strong and constitutional abilities is a necessary precondition, e.g., the educational therapist. His specific aptitudes at any rate are never given in the make-up of his personality but have to be acquired in personal crises, during which they emerge "new and quasi for the first time." His profession is founded on "suffered" abilities and talents.

Yet it seems to me that these and many more of the author's formulations will appear more acceptable if one can translate them into one's own familiar terminology. The chapters on disharmonic children and on "body-feeling," i.e., the inner experience of one's own somatic existence and functioning, show the author's unorthodox approach to old problems. If an individual is seized consciously by rhythms, as in dancing, then his "body-feeling" becomes vague and weak. In contrast, a state of being unconsciously imbedded in rhythms brings about a feeling of well-being; it increases the inner somatic experience so that the body is felt as a closed entity. This sensation also automatically closes down the bladder—so to speak—into the deepest sleep. In children, who are seized by, or given to, consciously felt rhythms the "body-feeling" is so feeble that the bladder cannot be closed during sleep. At least, the author considers this mechanism as one possible cause of enuresis, among many. He attributes to color-blindness an important role as a dynamic factor in disharmonic children and gives interesting contributions to the knowledge of personality disturbance as a reaction to the impairment of a sensory organ.

A last chapter on the Psychology of the Study of Human Behavior (Seelen-Beobachtung) deals with the task of perceiving and understanding "man" the individual. The author criticizes Kretschmer's typological approach, because it does not permit one to grasp the totality of "man's being" in the individual. Yet, if this never-to-be-finished task belongs somewhere, surely it belongs to philosophy, and not to psychology or any other science.

WALTER O. JAHRREISS

DAS KIND UND SEINE FRÜHESTE UMWELT. *Psychologische Praxis: Schriftenreihe für Erziehung und Jugendpflege, Number 6.*

By Fritz Stirnimann. S. Karger, Basel and New York. S. fr. 6.—(paper). 72 pp. 1947.

This publication gives a very detailed description of the child's development step by step from birth till the end of the first year. It is written by a pediatrician whose interest in the psychology of child development is evident and attested to by an index of his own publications. It is—by the way—the only one of the volumes of this series to be reviewed in this issue which helps the reader by including a brief bibliography and index. The general theoretical orientation follows von Monakow's biological teachings and von Uexkuell's formulation of the individual's specific sector of total environment, his "Umwelt" to which he adjusts himself and which in turn he influences.

WALTER O. JAHRREISS

KRITISCHE PHASEN DER KINDHEIT. *Psychologische Praxis: Schriftenreihe für Erziehung und Jugendpflege, Number 8.*

By Karl Heymann. S. Karger, Basel and New York. S. fr. 4.80 (paper). 52 pp. 1949.

Seven chapters, loosely joined together, are filled with observations and aphoristic statements: some critical, some original, and most of them stimulating. In the child's development crises are normal occurrences, and they are necessary for the growth of the personality. Critical periods are the times of transition from one developmental stage to the next, and regression to the behavior of a preceding phase is the common mode of reactions to existing conflicts. But antegression also occurs, as in the "precocious" child. Dreams of losing something precious are frequent in periods of transition: the years of early childhood seem paradise, but a paradise lost and not to be regained. During prepuberty and puberty, regression to "role" playing is not uncommon; yet the role is now built into an actual situation, into the frame of everyday reality. The playing, therefore, is apt to be misunderstood and taken for some kind of surprising misbehavior.

In a chapter on Drawings in Childhood, the author stresses the fact that the small child (two to six) is living in his own world, taking it for granted; yet he longs to understand the world of the grown-ups and to take part in their "reality." The child gropes for new ways of expression, like drawing and painting, in order to break the threatening isolation. It is an attempt at self-healing, and it should be used diagnostically and therapeutically.

Chapters on the school system as organism, on testing for occupational aptitudes, and on occupation and personality contain good suggestions and observations. The author describes a characteristic crisis of the European "apprentice." It is said to occur usually during the second year of apprenticeship and is interpreted as

the individual expression of the conflict between personal interest in work and workmanship and the demands of the machine to deny all personal interests.

WALTER O. JAHRREISS

THE GIFTED CHILD GROWS UP. *Twenty-Five Years' Follow-Up of a Superior Group. Genetic Studies of Genius, Volume IV.*

By Lewis M. Terman and Melita H. Oden, in association with Nancy Bayley, Helen Marshall, Quinn McNemar, Ellen B. Sullivan. Stanford University Press, Stanford; Geoffrey Cumberlege, Oxford University Press, London. $6.00. xiv + 448 pp. 1947.

A follow-up study by Terman of his original California group of gifted children in 1940 and 1945 has resulted in this the fourth volume in the now famous *Genetic Studies of Genius*. With this report we are brought up to date regarding the lives and achievements of more than a thousand people of superior intelligence who were selected as children by Terman 25 years ago for a comprehensive lifetime study. We find them now as adults about 35 years old, taking their places in their home communities, and with their adult careers well under way. The most general significant finding of the report is the group's continued superiority to the general population in virtually all phases of life activity.

The book has been well organized by the authors, who have also expertly summarized a prodigious quantity of data neatly and with objectivity. Interpretation has been held to a minimum, the authors preferring to have the facts, of which they provide a storehouse, speak for themselves.

This gigantic undertaking—a methodical, longitudinal study of genius—is now in its half-way period, plans having been made to continue it for another 25 years. It is remarkable to realize that almost all we reliably know and understand regarding children of superior intellectual endowment is directly or indirectly the result of Terman's pioneer work, of which this book is another ***in progress*** report. Terman has provided the background necessary for the development and implementation of the education and guidance of children of superior intelligence so as to prepare them better to shoulder the disproportionate responsibilities that fall on them—the responsibilities of self-fulfillment and community leadership.

JOSEPH C. FRANKLIN

THE PSYCHOANALYTIC STUDY OF THE CHILD. *Volume III/IV.*

Edited by Phyllis Greenacre, Heinz Hartmann, Edith B. Jackson, Ernst Kris, Lawrence S. Kubie, Bertram D. Lewin, Marian C. Putnam, Rudolph M. Loewenstein, Anna Freud Willie Hoffer and Edward Glover. International Universities Press, New York. $10.00. 493 pp.; ill. 1949.

This volume continues the series begun several years ago in which current papers that deal with psychoanalytic concepts related to children and their development are brought together. As in the preceding volumes (*Q.R.B.*, 23: 91, 1948), the papers are excellent, informative, and stimulating.

The collection covers a wide range, the papers being grouped under several headings. The first part is devoted to theoretical considerations. There are 3 papers on the development of aggression in this section. One, by Anna Freud, and entitled Aggression in Relation to Emotional Development; Normal and Pathological, is particularly interesting.

In the second section of the book are grouped the papers falling under Clinical Problems. This is by far the most dramatic part of the volume. Here many of the really first rate child analysts have given reports of their cases. To any reader oriented in the field of psychoanalysis, these are engrossing. Berta Bornstein reports in unusual detail The Analysis of a Phobic Child—Some Problems of Theory and Technique in Child Analysis. It covers the high points of a 3-year analysis of a 5½ year old boy with a severe school phobia. The child is a remarkable case and serves to illustrate the author's observations of the theoretical and technical implications involved. Editha Sterba, in her paper Analysis of Psychogenic Constipation in a Two-Year Old, is equally fascinating. Elisabeth R. Geleerd, Bruno Bettelheim, and Melita Sperling and others have also contributed papers to this section.

Part III is on psychoanalytic guidance work. Part IV is devoted to Problems of Group Psychology. Part V is a survey of the literature on psychogenic feeding problems; and Part VI is an historical report by Bertram D. Lewin on Child Psychiatry in the 1830's.

Once again, the reviewer is impressed by the continuity of thought and even of style which prevails throughout this yearbook. It is apparent that though the authors are widely separated geographically, they are intellectually united. This does not mean to imply sameness or repetitiousness. The authors are strong individuals, with new ideas to present, but they are working within the framework of traditional Freudian thought and that is the unifying factor.

HELEN ARTHUR

HUMAN BIOLOGY

SOCIETY, CULTURE, AND PERSONALITY: THEIR STRUCTURE AND DYNAMICS. *A System of General Sociology. Harper's Social Science Series.*

By Pitirim A. Sorokin. Harper & Bros., New York and London. $5.00. xiv + 742 pp. 1947.

In this patently monumental work, Sorokin "attempts to present a system of sociology as a generalizing science of sociocultural phenomena possessing its own set of referential principles, its own meaningful-causal method ... Little concerned with physical, biological, and other 'presociological' problems," he has confined himself to a study of "sociocultural phenomena in their structural and dynamic aspects." The author's method is scholarly, empirical, and rational and, while drawing on the experimental data of science, is frankly tentative, for he reminds us that in this area attempts at "absolute exactness" result "ordinarily in misleading preciseness acquired at the expense of approximate validity."

Sorokin's systemization of sociocultural phenomena is based on the interaction of two or more persons involving (a) society (organizations and groups of individuals), (b) culture (including goals, values, communications, norms, etc. and the agencies which "express and objectify" them), and (c) the personalities of the members "which are molded in their psycho-social, and also in part their biological, properties by the culture in which they are raised."

According to Sorokin, these components are inseparable and indivisible in his superorganic world. This interaction of the three basic items is lengthily and closely argued in a style considerably difficult to read. Those who are motivated to bring the social chaos and crises of our times into manageable dimensions in their thinking will find Sorokin's orientation provocative and rewarding.

JOSEPH C. FRANKLIN

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